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Ian BEVERIDGE

A TAXONOMIC REVISION OF THE GENERA *CITTOTAENIA* RIEHM, 1881, *CTENOTAENIA*, RAILLIET, 1893, *MOSGOVOYIA* SPASSKII 1951 AND *PSEUDOCITTOTAENIA* TENORA, 1976. (CESTODA : ANOPLOCEPHALIDAE).

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by
Ian. BEVERIDGE *

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INTRODUCTION

In an earlier revision of the anoplocephalid cestodes of Australian marsupials (Beveridge, 1976) it was found difficult to define the relationships of the genera *Progamotaenia* Nybelin, 1917, *Paramoniezia* Maplestone and Southwell, 1923 and *Phascolotaenia* Beveridge, 1976, revised or described in that work with the genera of the "*Cittotaenia* complex" most similar to them, in particular the genera *Mosgovoyia* Spasskii, 1951 and *Ctenotaenia* Railliet, 1893, as reviewed by Spasskii (1951). Prior to Spasskii's (1951) revision of the Anoplocephalidae, the species belonging to these two genera were placed within the large and obviously composite genus *Cittotaenia* (Riehm, 1881), as in the monograph by Baer (1927). Tenora (1976) indicated some of the shortcomings of Spasskii's earlier work and rearranged the species in order to overcome the obvious deficiencies.

However, the revisions of both Spasskii (1951) and Tenora (1976) suffer from the disadvantage that they are based more on a study of the literature rather than of the relevant specimens. Consequently, it was decided to undertake a full revision of the genus *Cittotaenia sensu* Baer (1927) working from existing collections of cestodes and providing new descriptions for all species involved, even though some of them are extremely well known. In this way it was hoped that some of the difficulties outlined earlier might be overcome.

Because many of the species formerly placed in the genus *Cittotaenia* by Baer (1927) have since been transferred to a wide variety of new and resurrected genera in two subfamilies (Spasskii, 1951, Tenora, 1976) as well a new species having been added to the genus the format of the present revision is somewhat unconventional. The genera *Cittotaenia* Riehm, 1881, *Ctenotaenia* Railliet, 1893, *Mosgovoyia* Spasskii, 1951 and *Pseudocittotaenia* Tenora, 1976 are dealt with in full. In addition, although the Australian representatives of the genus *Paramoniezia* were discussed by Beveridge (1976), *Pa. psittacea* (Fuhrmann, 1904) Spasskii, 1951 is also described in the present work as it originally belonged to the genus *Cittotaenia* (see Fuhrmann, 1904, 1921, Baer, 1927) and, as indicated by Beveridge (1976), does not belong in the genus *Paramoniezia*. Species transferred to genera other than those revised in the present paper have been described in full and their reclassification discussed and justified in detail.

Species with inadequate descriptions, incomplete or missing types which cannot be placed satisfactorily in any known genus are listed as *Cittotaenia sensu lato* with their original nomenclatural combinations, but are considered as *species incertae sedis* or *inquirenda*.

Source : MNHN, Paris

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ABSTRACT

The anoplocephalid cestode genera *Cittotaenia* Riehm, 1881, *Ctenotaenia* Railliet, 1893 and *Mosgovoyia* Spasskii, 1951 are revised. The genus *Ctenotaenia* Railliet, 1893 is upheld, with a single species, *Ct. marmotae* (Fröhlich, 1802). *Ct. citelli* (Kirshenblatt, 1939) and *Ct. avicola* (Fuhrmann, 1897) fall as synonyms of it. The genus *Mosgovoyia* Spasskii, 1951 is redefined with three valid species, *M. pectinata* (Goeze, 1782), *M. ctenoides* (Railliet, 1890) comb. nov. and *M. variabilis* (Stiles, 1895) comb. nov. The species *M. perplexa* (Stiles, 1895), *M. oitana* Sawada and Kugi, 1974 and *Cittotaenia wittei* Baer and Fain, 1955 are treated as synonyms of *M. pectinata* (Goeze, 1782). The genus *Neoctenotaenia* Tenora, 1976 is a synonym of *Mosgovoyia* Spasskii, 1951. The genus *Pseudocittotaenia* Tenora, 1976 is retained for *P. praecoquis* (Stiles, 1895) comb. nov., with *Cittotaenia megasacca* Smith, 1951 as its synonym, and *P. glandularis* sp. nov. created for the species described by Smith (1951) as *Cittotaenia praecoquis* (Stiles, 1895). The genus *Cittotaenia* Riehm, 1881 is retained provisionally within the sub-family Monieziinae Spasskii, 1951, with *C. denticulata* (Rudolphi, 1804) as the type species, and *Cittotaenia oiscaciae* (Spasskii, 1951) comb. nov. *Cittotaenia psittacea* Fuhrmann, 1904 is made the type and only species of a new genus *Stringopotaenia* gen. nov. *Cittotaenia rhea* Fuhrmann, 1904 and *C. bequaerti* Vigueras, 1943 are both transferred provisionally to the genus *Moniezia* Blanchard, 1891. *C. taehyglossi* Johnston, 1913 is considered a *species incertae sedis*. *C. quadrata* von Linstow, 1904, *C. dratchynskii* Romanovitch, 1915 and *C. krishnai* Nama, 1972 are considered *species inquirendae*.

MATERIALS AND METHODS

The present revision is based on cestode collections in various museums and universities as well as on specimens in the collections of private individuals. The following abbreviations of institution names are used in the text :

* Institut de Zoologie, Université de Neuchâtel, Suisse.

Source : MNHN, Paris

BM	British Museum (Natural History).
HCIOC	Helminth Collection of Instituto Oswaldo Cruz, Rio de Janeiro, Brasil.
LSTM	Liverpool School of Tropical Medicine, collection currently on loan to the University of Neuchâtel.
NUE	Nara University of Education, Japan.
UAHC	University of Adelaide, Department of Zoology, Helminth Collection currently held in the South Australian Museum, Adelaide, Sth. Australia.
UMVS	University of Melbourne, School of Veterinary Science, Australia.
UN	University of Neuchâtel, Switzerland.
UNMC	University of Nebraska, Manter Collection, U.S.A.
USNM	United States National Museum Parasite Collection, U.S.D.A. Beltsville, Maryland, U.S.A.
UU	University of Utah, Dep. of Biology, Salt Lake City, U.S.A.

The number of specimens examined is shown where it is known. In the case of some large species for which only slide material was available, the number of worms examined is not known. Museum numbers referred to in the text under material examined may designate a single specimen or a series of specimens.

Host and geographical records have been tabulated for clarity when they are extensive. The literature cited is not exhaustive as, in the case of the better known species, much of the literature is of no taxonomic significance. Works with incomplete host or parasite identifications (*eg. Lepus* sp., *Cittotaenia* sp.) have been disregarded as have those with no or vague locality records, unless the host is reported as new. Works merely repeating earlier literature (where identifiable) have been omitted.

Published measurements are tabulated. Synonymies prior to 1896 are those of Stiles (1896), and only principal references are given. Detailed synonymies of these parasites as far as 1912 can be found in Stiles and Hassall (1912).

Records given to the present day are not exhaustive. Works such as general parasitology texts or papers in which only a passing reference is made to the parasite in question have been disregarded.

Because of numerous changes in botb host and parasite names, tables summarising bost and geographical data for a parasite have original host determinations listed as synonyms of the current names and indicate the original name applied to the parasite recorded.

The following texts have been used as a basis of host nomenclature : — Ellerman and Morrison-Scott (1951), Cabrera (1961) and Hall and Kelson (1959).

Source : MNHN, Paris

DESCRIPTIONS

Family ANOPLOCEPHALIDAE Kholodkovskii, 1902

1. — Subfamily ANOPLOCEPHALINAE Blanchard, 1891

Genus *CTENOTAENIA* Railliet, 1893

Ctenotaenia Railliet, 1893 : 278 ; Spasskii, 1951 : 256-275 ; Tenora, 1976 : 9-10.
Cittotaenia Riehm, 1881a : 200 *pro parte* ; Stiles, 1896 : 170 ; Baer, 1927 : 49 ; Yamaguti, 1959 : 376.

Types species. *Ctenotaenia marmotae* (Fröhlich, 1802). Only species.

Diagnosis. Cestodes of moderate size. Strobila broad, ribbon-like. Scolex small, unarmed. Suckers unarmed. Proglottides numerous (over 100 in gravid strobilae), craspedote, greatly extended transversely. Longitudinal osmoregulatory canals paired. Transverse canal connects left and right ventral canals at posterior margin of each proglottis. Genital ducts cross longitudinal osmoregulatory canals dorsally. Genitalia paired. Cirrus sac opens to genital atrium anterior to vagina. Cirrus sac dorsal to vagina on both sides of strobila. Internal and external seminal vesicles present. Testes numerous, anterior and posterior to uterus in single band, medial to female genitalia. Seminal receptacle present. Ovaries situated in lateral quarters of proglottis medulla. Single transverse uterus in each proglottis. Uterus does not cross longitudinal osmoregulatory canals. Gravid uterus sac-like with anterior and posterior diverticula. Pyriform apparatus present. Parasites of Sciuridae (Rodentia).

Remarks. The genus *Ctenotaenia* was resurrected by Spasskii (1951) for *Ct. marmotae* and seven other species he wbished to distinguish generically from *Cittotaenia* into which all had previously been placed (Baer, 1927). However, even Spasskii (1951) admitted that the taxonomy of the genus was unsatisfactory and Tenora (1976) subsequently reduced the number of species removing most to other genera. *Ct. asiatica* Tokobajev and Erkulov, 1966 was admitted as a valid species by Tenora and Hörning (1972) but was later transferred to the genus *Paranoplocephala* Lühe, 1910, a genus with a single set of genitalia per proglottis, by Tenora in 1976. The present revision reduces the number of valid species to one, *Ct. citelli* (Kirshenblatt, 1939) and *Ct. avicola* (Fuhrmann, 1827) falling as synonyms of *Ct. marmotae*.

The genus *Ctenotaenia* differs from *Mosgovoyia* and *Pseudocittotaenia* in that the testes are not entirely posterior to the uterus but occur both anterior and posterior to it. *Ctenotaenia* differs from *Progamotaenia*, *Phascolotaenia* and *Paramonieza* (*sensu* Beveridge, 1976) in that the testes in *Ctenotaenia* are restricted to the area between the female genitalia.

Source : MNHN, Paris

Ctenotaenia marmotae (Fröhlich, 1802)
Figs 1-10, Tables 1-3.

Taenia marmotae Fröhlich, 1802 : 77-79, pl. 2, figs 17-20.
Moniezia marmotae (Fröhlich, 1802) Blanchard, 1891 : 187, 444, 461-467, figs 31-35.
Taenia pectinata Goeze, 1782 *pro parte*, Rudolphi, 1804 : 108.
Cittotaenia pectinata (Goeze, 1782) Stiles and Hassall, 1896b : 407 *pro parte*, Baer, 1927 : 55.
Cittotaenia pectinata citelli Kirshenblatt, 1939 : 116-128.
Cittotaenia citelli (Kirshenblatt, 1939) Kirshenblatt, 1947 : 115-118.
Ctenotaenia citelli (Kirshenblatt, 1939) Spasskii, 1951 : 263-267, fig. 123.
Cittotaenia avicola Fuhrmann, 1897 : 108-117, pl. 5, figs 1-8.
Ctenotaenia avicola (Fuhrmann, 1897) Spasskii, 1951 : 260-263, fig. 122.

Types. From *Marmota marmota* Linnaeus, 1758, location unknown.

Material examined.

From *Marmota marmota* Linnaeus, 1758 : 1 specimen, Briançon, France, September 1887 from collection of R. Blanchard, now in collection of C. Joyeux, UN ; 2 specimens without collection data, UN ; 80 specimens, Bevers, Switzerland, 14 July 1964, G. Zelenka, UN.

From *Citellus major erythrogenys* Brandt, 1841 : 6 specimens, Siberia, U.S.S.R., no other data, UN.

From *Anas* sp. : types of *Cittotaenia avicola*, no other data, UN.

Description. Large, broad, ribbon-like worms, anterior extremity tapering markedly. Scolex small, globular, distinctly demarcated from strobila in contracted specimens, rounded anteriorly and merging into strobila in relaxed specimens. Neck absent. Proglottides craspedote narrow, straight-edged velum overhanging adjacent proglottis. Mature proglottides much wider than long with approximate length : width ratio 1 : 10-1 : 17. Gravid proglottides with approximate length : width ratio 1 : 10-1 : 32. Longitudinal musculature weakly developed, arranged in two circles of muscle bundles in cortex. Outer muscle bundles oval or circular in transverse section, small, composed of 5-35 muscle fibres. Bundles of inner ring smaller, less regularly arranged, composed of 2-10 muscle fibres. Transverse muscles filiform, forming narrow band internal to longitudinal muscles. Dorso-ventral muscle fibres fine, crossing medulla and cortex at regular intervals. Ventral longitudinal osmoregulatory canal wider than dorsal canal, situated medial to dorsal canal. Transverse canal connects left and right ventral canals at posterior margin of each proglottis. Dorsal and ventral canals of each side of strobila loop laterally at level of suckers then return towards mid-line. Dorsal canals from each side join in mid-line and continue anteriorly as pair of ducts, similarly ventral canals of both sides. Annular anastomosis connects four ducts at anterior extremity of suckers. Genital atrium prominent, forming large ovoid sinus, opening to exterior in posterior half of lateral proglottis margin, dividing margin in ratio 1 : 1.5- 1 : 3. Cirrus sac elongate, pyriform, thick-walled, usually reaching or crossing longitudinal osmoregulatory canals. In immature proglottides, cirrus sac may not reach osmoregulatory canals. Cirrus long, coiled within cirrus sac, distal region unarmed, proximal region heavily armed with rows of spines. On everted cirri, spines longest at distal extremity, diminishing in size near mid-region. Spines on proximal region very short. Cirrus surrounded by prostatic cells. Large, ovoid internal seminal receptacle present. External seminal vesicle elongate, slightly coiled. Vas deferens narrow. Testes numerous, distributed in 3-6 horizontal and 2-4 dorsoventral layers. Testes invariably lie in single field between female genital glands on dorsal aspect of medulla. Occasionally testes overlie medial extremity of ovary but never lie lateral to ovary. Testes situated both

Source : MNHN, Paris

anterior and posterior to uterus. Distal vagina forms ovoid atrium with hairy lining. Mid-region of vagina tube-like, thin-walled. Junction of tube with atrium surrounded by muscular sphincter. Vagina merges into elongate, pyriform seminal receptacle, extending along posterior margin of proglottis, dorsal to ovary, to poral margin of vitellarium. Ovary fan-shaped, composed of numerous clavate lobules, situated on ventral aspect of medulla. Vitellarium ovoid or reniform, lobulate, posterior and dorsal to ovary. Mehlis' gland spherical, posterior to ovary, dorsal to vitellarium. Uterus tube-like, transverse, single, in middle of proglottis, passing dorsal to ovary, anterior to vitellarium and seminal receptacle. Gravid uterus with numerous anterior and posterior diverticula. Uterus never extends laterally beyond longitudinal canals. Egg spherical, thick-shelled. Pyriform apparatus terminates in two elongate horns.

Vestigial, supernumerary vitellaria present in many proglottides, of variable size, posterior to uterus, connected to uterus in some instances by narrow duct. One to three, usually two, extra vestigial vitellaria per proglottis.

REMARKS. Although a comparatively well-known species, the descriptions and illustrations of it in the literature are rather poor. Stiles (1896) gave a brief description of the parasite based on Blanchard's material, and his description was subsequently used by Spasskii (1951), though the figures which Spasskii reproduced from Stiles' work and labelled as *Ct. marmotae* (Fg. 120, p. 258) are in fact Stiles' drawings of *Cittotaenia denticulata* (Rudolphi, 1804). Spasskii and Shalajeva (1961) gave an improved description of the parasite based on material from *Marmota bobak*, whilst Tenora and Hörning (1972) gave a detailed bibliographic review of the species but did not deal in detail with its morphology. Tenora (1976) further discussed the parasite but some of the morphological observations he offers appear to be in error. He commented on the distribution of the testes thus (Tenora, 1976, p. 9): "The testes in the strobila of *C. marmotae* and *C. citelli* are situated always above the tubular uterus. They fill the upper half of proglottides and in fully formed bermaphrodite proglottides they may even reach under the uterus". The statement appears inconsistent and as illustrated in fig. 10, testes lie both anterior and posterior to the uterus, hence Tenora's (1976) observations cannot be accepted. Tenora (1976) also used this feature as a differentiating character in a key to the genera of the Anoplocephalinae (pp. 15-16). In some mature proglottides examined during the present work, the transverse osmoregulatory canal was greatly distended, displacing the testes to the anterior half of the proglottis, much as is shown in Plate 11 fig. 7 of Stiles (1896). In the case mentioned testes were still distributed both anterior and posterior to the uterus, but the uterus was not readily seen and it is possible that Tenora (1976) was looking at a similar abnormality in his material and mistook the transverse osmoregulatory canal for the uterus.

Blanchard (1891) described and illustrated additional osmoregulatory canals to those found in the present study. However, Berthoud's (1966) description and drawing of the osmoregulatory system agree with the current description as do the observations of Tenora and Hörning (1972).

In the current revision, *Ct. citelli* (Kirshenblatt, 1939) is considered to be a synonym of *Ct. marmotae*. Originally described from *Citellus citellus xanthoprymnus* by Kirshenblatt (1939) the species was subsequently found to be widely distributed in Russia, occurring also in *Citellus pygmaeus* and *C. citellus dauricus* and was described in some detail by Spasskii (1951). Although the types were not available for study, specimens from *Citellus major erythrogenys* from Siberia, together with Spasskii's detailed description permit the re-assessment of the taxonomic position of the species. Spasskii (1951) concluded that *Ct. citelli* was very similar to *Ct. marmotae* but that they differed in two significant respects, namely that the cirrus of *Ct. citelli* was heavily armed whilst that of *Ct. marmotae* was not, and that there were more testes per proglottis in *Ct. citelli*. The cirrus of *Ct. marmotae* is in fact heavily armed, as is shown in figs 2 and 5 though this feature was not mentioned by Stiles (1896) upon whose description Spasskii (1951) relied. Spasskii and Shalajeva (1961) subsequently redescribed *Ct. marmotae* from *Marmota bobak* and illustrated a heavily armed cirrus. Consequently the supposed lack of cirrus armature in *Ct. marmotae* cannot be used to distinguish it from *Ct. citelli*.

The number of testes per proglottis in *Ct. citelli* has been recorded as 150-200 compared with 100-160 for *Ct. marmotae* (Table 1). In the present revision the number of testes per proglottis was

Source : MNHN, Paris

TABLE 1. — MEASUREMENTS of *CTENOTAENIA MARMOTAE* (in mm).

Author	Blanchard (1891)	Stiles (1896)	Fuhrmann (1897)	Spasskii & Salajeva (1961)	Berthoud (1966)	Tenora & Hörning (1972)	Spasskii (1951)	Present description	
Taxon described	*M. marmotae*	*C. marmotae*	(*Ct. avicola*)	*Ct. marmotae*	*C. pectinata*	*Ct. marmotae*	(*Ct. citelli*)		
Host	*M. mormota*	*M. marmota*	*Anas* sp	*M. bobak*	*M. marmota*	*M. marmota*	*C. pygmaeus*	*M. marmota*	*C. erythrogeny*[s]
Length	56-112	112	150-220	150	60	62-125	100-450	43-94	— *
Width	11	5-13	10	17	8-15	8-16	8-13	9-13	6-16
Scolex diameter	0.55-0.63 × 0.80-0.84	0.8 × 0.5 -0.6	0.8	0.60-1.0	0.8	0.60-0.98	0.46-0.98	0.7-1.0	0.76-0.93
Sucker diameter	0.12		0.33	0.35	0.24	0.18-0.28	0.21-0.30	0.28-0.35	0.23-0.32
Mature proglottis								7.0 × 3.5	5.1-7.0 × 0.4
Gravid proglottis								7.5-10.0 × 0.6-0.7	4.3-16 × 0.45-0.50
Cirrus sac		0. 5× 0.17	1.0 × 0.12			0.70 × 0.18	0.45-0.75 × 0.12-0.18	0.53-0.95 × 0.15-0.20	0.42-0.55 × 0.12-0.15
Internal seminal vesicle								0.37-0.60 × 0.10-0.16	0.30-0.48 × 0.12-0.15
External seminal vesicle							0.42-0.55 × 0.17-0.18	0.35-0.44 × 0.10-0.17	0.33-0.40 × 0.10-0.16
No. testes		100-150	120-140	120-150	160	125-160	150-200	116-166	104-187
Testis size			0.068				0.11	0.06-0.12	0.06-0.13
Seminal receptacle			1.0				1.2 × 0.3-0.4	0.7-0.8 × 0.25	0.3-1.3 × 0.15-0.30
Ovary			0.8				0.8-1.4	0.69-1.00 × 0.25-0.35	0.63-0.85 × 0.27-0.32
Vitellarium								0.20-0.38 × 0.30-0.35	0.3-0.45 × 0.10-0.15
Mehlis' gland							0.12	0.12	0.10
Dorsal osmoregulatory canal								0.04-0.06	0.02-0.04
Ventral osmoregulatory canal							0.03-0.30	0.12-0.14	0.06-0.26
Egg	0.048-0.060	0.048-0.060	0.054	0.050	0.055-0.064	0.05-0.064	0.035-0.050	0.05	0.03
Pyriform apparatus			0.018		0.025 × 0.04			0.03	—
Oncosphere	0.023		—	0.018-0.020		0.02-0.04		0.015	—

* Mounted specimens only available.

Source : MNHN, Paris

TABLE 2. — TESTIS NUMBER IN 5 PROGLOTTIDES FROM EACH OF 4 STROBILAE OF *CTENOTAENIA MARMOTAE*.

	HOST			
	Marmota marmota L.		*Citellus major erythrogenys* (Brandt)	
Strobila	1	2	3	4
No. testes	166	140	128	115
Per	133	135	163	138
Proglottis	129	125	187	116
	140	159	166	104
	151	116	165	145

TABLE 3. — HOST RECORDS OF *CTENOTAENIA MARMOTAE*

HOST	LOCALITY	REFERENCE
Marmota marmota Linnaeus, 1758	Briançon, France	Blanchard (1891)
	Vaud, Valais, Switzerland	Galli Valerio (1918, 1923, 1926, 1930a, b, 1931, 1933, 1935)
	Vaud, Switzerland	Fuhrmann (1926)
	Vaud, Switzerland	Schweitzer (1949).
	Switzerland	Schweitzer and Burgisser (1949)
	Valais, Switzerland	Bouvier *et al.* (1959)
	Valais, Uri, Graübunde, Fribourg, Berne, Switzerland	Hörning (1969)
	Swiss Alps	Hörning and Tenora (1971) Tenora and Hörning (1972)
	Austria	Jettmar and Anschau (1951)
	Pöllatal, Austria	Sixl (1975)
Marmota marmota latirostris Kratochil, 1961	Czechoslovakia	Tenora (1961)
Marmota marmota baibacina Brandt, 1843	Kazakhstan, USSR	Gvozdev and Kapitonov (1966)
Marmota bobak Muller, 1776	Kazakhstan, USSR	Gvozdev and Kapitonov (1966)
Marmota bobak tshaganensis Bashanov, 1930	Kazakhstan, USSR	Spasskii and Shalajeva (1961)
Citellus citellus	Armenia, USSR	Kirshenblatt (1939)
zanthoprymnus Bennett, 1835	Armenia, USSR	Akumian (1948)
Citellus citellus dauricus Brandt, 1843	USSR	Kirshenblatt (1947)
Citellus pygmaeus Pallas, 1179	USSR	Kirshenblatt (1947), Spasskii (1951)
Citellus suslicus	Ukraine, USSR	Kadenatsii (1957) (in Sharpilo, 1966)
Güldenstaedt, 1770	Ukraine, USSR	Sharpilo, 1961
	Byelorussia, USSR	Arzamasov *et al.* (1966)
« *Anas* sp. » ?	Switzerland	Fuhrmann (1897)

Source : MNHN, Paris

not found to differ significantly between the two forms. The testes in these cestodes are not always easy to count accurately as they lie in several layers and the difficulties are increased by the thickness of the cortex and hence the general opacity of the worms. The number of testes in a series of adjacent proglottides from several strobilae indicates the high level of variation which can occur within a single strobila (Table 2). Although statistical data for anoplocephalids are limited, Beveridge (1974) has shown that in the case of *Taenia pisiformis* (Bloch, 1780), at least 50 % of the variability in testis number in a population can be ascribed to within-strobila variation. Since a similar high level of variability occurs in strobilae of *Ct. mormotae* it is not considered valid to distinguish *Ct. citelli* on the basis of number of testes per proglottis. Table 1 also indicates that no other valid quantitative differences occur between these taxa. Spasskii and Shalajeva (1961) argued that *Ct. marmotae* and *Ct. citelli* should be maintained as separate since they inhabit different host genera. However, both the genus *Marmota* and the genus *Citellus* belong to the family Sciuridae and the ranges of the two genera even in the present day are contiguous or overlap so that allopatry cannot be used as a criterion to distinguish the species. Consequently *Ct. citelli* has been treated as a synonym of *Ct. marmotae*.

Cittotaenia avicola Fuhrmann, 1897 was described from specimens held in the Geneva Natural History Museum and labelled initially as "*Taenia lanceolata* Goeze" and as having been collected from a duck, *Anas* sp. Spasskii (1951) transferred Fuhrmann's species to the genus *Ctenotaenia* noting its close similarity with *Ct. citelli* but maintaining it as a valid species because of differences in the number of testes per proglottis. It is evident from a re-examination of the types that *Ct. avicola* is a synonym of *Ct. marmotae*, a mistake presumably having been made in the original label. Fuhrmann (1897) commented on the close similarity of his new species to *Ct. marmotae* (then *Cittotaenia marmotae*) but decided, erroneously, that the cirrus sac was more like that of *Mosgovoyia pectinata* (Goeze, 1782) (formerly *Cittotaenia pectinata* (Goeze, 1782)) and consequently placed *Ct. avicola* as a new species intermediate between the "*marmotae*" and "*pectinata*" groups of the genus *Cittotaenia*.

There are two other records of *Ct. avicola* in the literature. Meggitt (1927) identified a cestode from Sommett's jungle fowl, *Gallus sonnerati* Temminck, 1813 as "*C. ? arvicola*" apparently intending *C. avicola*, however the specimen was incomplete and could not be fully identified. Southwell (1930) reported that he had referred to this species some specimens from an Impeyan pheasant, *Lophophorus impejanus* (Latham, 1790), but that on subsequent examination an armed rostellum was detected and the cestodes were re-identified as *Cotugnia margareta* Beddard, 1916. He suggested that Meggitt's specimens might also belong to this species. Both records can now be disregarded as *Ct. avicola* falls as a synonym of *Ct. marmotae*.

Genus *MOSGOVOYIA* Spasskii, 1951

Mosgovoyia Spasskii, 1951 : 286-297 ; Yamaguti, 1959 : 383 ; Tenora, 1976 : 17.
Cittotaenia Riehm, 1881a *pro parte* Joyeux and Baer, 1961 : 550..
Neoctenotaenia Tenora, 1976 : 13.

Type Species. *Mosgovoyia pectinata* (Goeze, 1782).

Diagnosis. Cestodes of moderate size. Strobila broad, ribbon-like. Scolex small, unarmed. Suckers unarmed. Proglottides numerous (over 100 in gravid strobilae), craspedote, greatly extended transversely. Longitudinal osmoregulatory canals paired. Transverse canal connects left and right ventral canals at posterior margin of each proglottis. Genital ducts cross longitudinal osmoregulatory canals dorsally. Genitalia paired. Cirrus sac opens to genital atrium anterior to vagina. Cirrus sac dorsal to vagina on both sides of strobila. Internal seminal vesicle present. External seminal vesicle absent. Testes numerous, entirely posterior to uterus in single hand or two groups, either restricted to area between female genitalia or extending laterally beyond them. Distal vagina

Source : MNHN, Paris

surrounded by glandular cells. Seminal receptacle present. Ovaries situated in lateral quarters of proglottis medulla. One or two transverse, tubular uteri per proglottis, either restricted to medulla or crossing longitudinal osmoregulatory canals dorsally, terminating posterior to cirrus sac and vagina. Gravid uterus sac-like with or without anterior and posterior diverticula Pyriform apparatus present. Parasites of Leporidae (Lagomorpha) and rarely Sciuridae (Rodentia).

KEY TO SPECIES OF *Mosgovoyia*

1. Uterus in mature proglottides reaching but never crossing longitudinal osmoregulatory canals..... *pectinata*

Uterus in mature proglottides invariably extending laterally beyond osmoregulatory canals.... 2

2 (1). Testes extend laterally beyond female genitalia, usually in two groups; cirrus sac broad, ellipsoidal. *ctenoides*

Testes restricted to area between female genitalia, almost invariably in single band; cirrus sac narrow, elongate..... *variabilis*

REMARKS. The genus *Mosgovoyia* was established by Spasskii (1951) for *Cittotaenia pectinata* (Goeze, 1782) and *C. perplexa* (Stiles, 1895). Spasskii (1951) also designated a specimen of *C. pectinata* described from a viscaca by Joyeux and Dollfus (1931) as a new species, *Mosgovoyia viscaciae*. The taxonomic history of the former two species is of some importance to the present revision and hence it will be reviewed in some detail.

In Stiles' revision (Stiles, 1896), the species *Cittotaenia pectinata*, *C. perplexa* and *C. variabilis* (Stiles, 1895) constituted the so-called "*pectinata*" group within the genus, being characterised by the narrow, elongate cirrus sac. Hall in 1908 added a further species, *C. mosaica*, differentiated from *C. pectinata* by the small size of the cirrus sac and by mosaic markings on the strobila. However, Douthitt (1915) found that Stiles was mistaken in his measurements of the cirrus sac of *C. perplexa* and that *C. mosaica* was a synonym of *C. perplexa*. Douthitt (1915) also established the subspecies *C. pectinata americana* for American representatives of the species.

Baer (1927) recognised only three valid species of *Cittotaenia* in lagomorphs, namely *C. denticulata* (Rudolphi, 1804), *C. ctenoides* (Railliet, 1890) and *C. pectinata*, considering the last named species to be extremely variable and placing as synonyms to it not only *C. variabilis* and *C. perplexa* but also *C. marmotae* and *C. quadrata* von Linstow, 1904. Baer (1927) also suppressed the subspecies *C. pectinata americana*.

Rees (1933a) gave a detailed account of the morphology of *C. pectinata* collected in Wales and designated her material as a new subspecies *C. pectinata europea*. Because of the confusion arising from Baer's (1927) revision of the "*pectinata*" group, Arnold (1938) undertook yet another review based on new material and reinstated *C. perplexa* and *C. variabilis* as well as *C. pectinata americana* as valid taxa.

Spasskii (1951) removed the type species of the genus *Cittotaenia*, *C. denticulata* to the subfamily Moniezziinae because it possesses a reticulated uterus, and transferred *C. ctenoides* and *C. variabilis* to the resurrected genus *Ctenotaenia*, thereby breaking up the so-called "*pectinata*" group. The genus *Mosgovoyia*, created to contain *C. pectinata* and *C. perplexa*, was distinguished from other genera by the occurrence of testes posterior to the uterus, extending laterally to the female genitalia on either side of the strobila and by the presence of accessory osmoregulatory canals connecting the transverse canals of adjacent proglottides. Spasskii (1951) also noted that a nominal subspecies of *M. pectinata* had never been designated and hence proposed the name *C. pectinata pectinata* for the European form of the species.

The present revision fails to support Spasskii's (1951) arrangement of the genus *Mosgovoyia* although retaining it as a valid genus. It is to Spasskii's credit that he recognised the composite nature of the genus *Cittotaenia sensu* Baer, 1927 and removed *C. denticulata* making a revision of the genus possible. However, the way in which Spasskii (1951) distributed the remaining species of *Cittotaenia* between

Source : MNHN, Paris

the genera *Ctenotaenia* and *Mosgovoyia* is inconsistent. In the type species of the genus *Ctenotaenia*, *Ct. marmotae*, the distinguisbing characteristic is the distribution of the testes both anterior and posterior to the uterus but limited to tbe area between the female genitalia. By contrast, in members of the genus *Mosgovoyia sensu* Sapsskii (1951), the testes lie in a band entirely posterior to the uterus but extend laterally beyond the female genitalia. In support of this generic distinction, Spasskii (1951) argues convincingly that tbe genus *Mosgovoyia* has been derived by a doubling of the genitalia from species of the genus *Schizorchis* Hansen, 1948 in whicb the testes lie entirely posterior to the uterus and the bosts of which are members of the genus *Ochotona*, also Lagomorpba. The genus *Ctenotaenia* was considered to have arisen by doubling of the genitalia of species of the genus *Paranoplocephala* Lühe, 1910 in which the testes lie aporal to tbe female genitalia. Species of both *Ctenotaenia* and *Paranoplocephala* parasitise rodents. If tbese arguments from morphological features, bost distributions and possible phylogenetic affinities are valid, then tbe otber lagomorph parasitising species *C. variabilis* and *C. ctenoides* which Spasskii (1951) transferred to the genus *Ctenotaenia* but which also have the testes situated entirely posterior to the uterus should also be transferred to the genus *Mosgovoyia*. Tbis cbange bas been made in the present revision. The revised genus *Mosgovoyia* is distinguished from related genera principally by the distribution of testes, but also by the morpbology of the female genital ducts since the distal vagina is surrounded by layers of glandular cells and the vagina leads into a thin-walled, elongate seminal receptacle. Other anoplocephaline genera (*Progamotaenia* Nybelin, 1917, *Phascolotaenia* Beveridge, 1976) also have morphologically distinctive female genital ducts wbich are of considerable taxonomic use.

M. pectinata differs from the other species currently placed in the genus by the possession of accessory osmoregulatory canals and Spasskii (1951) used it as a generic character. Although the features of the osmoregulatory system have been considered as having considerable phyletic, and hence taxonomic significance (Wardle, 1932), giving them generic significance in the present classification leads to tbe impossibility of successfully assimilating several other characters which may be of at least equal importance. Although the existence of accessory canals in *Schizorchis ochotonae* Hansen, 1948 as well as in *M. pectinata* was one factor involved in the choice of tbis feature as a generic character, they do not occur in all species of *Schizorchis*. They apparently exist in *S. ochotonae* and *S. yamashitai* Rausch, 1963 but have not been described in either *S. caballeroi* Rausch, 1960 or *S. altaica* Gvozdev, 1951 (Hansen, 1948, Spasskii, 1951, Rausch, 1960, 1963, Rausch and Ohbayashi, 1974). In order to avercome the difficulty, Tenora (1976) created the genus *Neoctenotaenia* for the species *M. ctenoides* and *M. variabilis*. In the present revision the presence of accessory osmoregulatory canals is not considered a valid generic criterion and hence the genus *Neoctenotaenia* is treated as a synonym of *Mosgovoyia*.

Mosgovoyia pectinata (Goeze, 1782)
Figs 11-25, Tables 4-5

? Taenia aeutissima Pallas, 1781 : 75-81, pl. 3, fig. 25.
Taenia leporina Rudolphi, 1810 : 82.
Taenia pectinata Goeze, 1782 : 363-368, pl. 27, figs 7-13.
? Alyselminthus pectinatus (Goeze, 1782) Zeder, 1800 : 246-249.
? Halysis pectinata (Goeze, 1782) Zeder, 1803 : 332.
Dipylidium pectinatum (Goeze, 1782) Riehm, 1881a : 200, 575-583, pl. 5, figs 4, 14, pl. 6, figs 4, 7.
Moniezia pectinata (Goeze, 1782) Blanchard, 1891 : 187, 445, 450-452, 457-460, figs 26-30.
Ctenotaenia pectinata (Goeze, 1782) Railliet, 1893 : 278-279.
Cittotaenia pectinata (Goeze, 1782) Stiles and Hassall, 1896b : 407.
Cittotaenia pectinata americana Doutbitt, 1915 : 47, pl. 16, fig. 45.
Cittotaenia pectinata europea Rees, 1933a : 250.
Cittotaenia pectinota septentrionalis Romanovitch, 1915 : 453.
Mosgovoyia pectinata (Goeze, 1782) Spasskii, 1951 : 287-295, figs 135-139.

Source : MNHN, Paris

Mosgovoyia pectinata pectinata Spasskii, 1951 : 289-295.
Mosgovoyia pectinata americana (Douthitt, 1915) Spasskii, 1951 : 295.
Mosgovoyia pectinata europaea (Rees, 1933) Yamaguti 1959 : 383.
Ctenotaenia perplexa Stiles, 1895 : 345.
Cittotaenia perplexa (Stiles, 1895) Stiles and Hassall, 1896b : 407.
Mosgovoyia perplexa (Stiles, 1895) Spasskii, 1951 : 295-296, fig. 140.
Cittotaenia bursaria von Linstow, 1906 : 164, 184, pl. 2, figs 39-40.
Cittotaenia mosaica Hall, 1908 : 691-699, figs 1-6.
Cittotaenia wittei Baer and Fain, 1955 : 11-13, figs 2-3.
Neoctenotaenia wittei (Baer and Fain, 1955) Tenora, 1976 : 13.
Mosgovoyia vitana Sawada and Kugi, 1974 : 264-266, figs 9-15.

TYPES. Whereabouts unknown.

MATERIAL EXAMINED.

From *Oryctolagus cuniculus* Linnaeus, 1758. 5 specimens Milford, Surrey, England, 8 August 1974, A. Mead-Briggs, UN and UMVS ; 1 specimen Essex, England, 9 June 1963, R. J. Knowles, BM 1963.7.8.75 ; Cardiganshire, Wales, G. Rees, BM ; Iniskea North, Mayo, Ireland, R. J. Knowles, September 1967, BM 1970.4.17.27-28 ; 1 specimen, Newton, Mayo, Ireland, September 1969, R. J. Knowles, BM 1970.4.17.29 ; Germany, no other data, USNM 1234-1237 ; 1 specimen, N. Ireland, no date, H. Shatowy, BM 1976.5.14.3.

From *Lepus europaeus* Pallas, 1778. 1 specimen, Nancy, France, 7 December, 1905, C. Joyeux, UN.

From *Lepus europaeus crawshayi* de Winton, 1899 (syn. *L. crawshayi*). 1 specimen Mukana, Zaïre, no date, UN (type of *Cittotaenia wittei*).

From *Lepus europaeus saxatilis* Cuvier, 1823. (syn. *L. saxatilis*). 2 specimens, Transvaal, South Africa, 8 March 1957, F. Zumpt, BM 1958.8.4.135-137.

From *Lepus timidus* Linnaeus, 1758. 1 specimen Isle of Mull, Scotland, 22 June 1953, BM 1963.11.26.11-20 ; 1 specimen Anagh, Mullet, 28 August 1969, R. J. Knowles, BM 1970.4.17.30 ; 4 specimens, Bernese Oberland, Switzerland, 21 November, J. Codonrey, UN.

From *Lepus capensis* Linnaeus, 1758. Kenya, no other data, USNM 54538 ; Sudan, no other data, USNM 54507.

From *Lepus nigricollis* Cuvier, 1823. Nedenkuni, Sri Lanka, no other data, UN (types of *Cittotaenia bursaria*).

From *Lepus nigricollis ruficaudatus* Geoffroy, 1826. (syn. *L. ruficaudatus*). 10 specimens, Songara, India, November 1920 ?, ? T. Southwell, LSTM.

From *Lepus americanus* (Erxleben, 1777). Maine, USA, no other data, USNM 44683 ; Alaska, USA, no other data, USNM 30098 ; Ontario, Canada, 19 July 1932, D. G. Mackintosh, USNM 42519 ; Frank's Bay, Ontario, Canada, 20 June, 1932, D G. Mackintosh, USNM 42520 ; 1 specimen St. Edward's Is., Canada, C. Bursey, UN.

From *Lepus americanus macfarlani* Merriam, 1900. 1 specimen, Mile 81, Taylor Highway, Alaska, 10 August 1963, R. L. Rausch ; 1 specimen, same locality and collector, 11 August 1963 both in Colln. R. L. Rausch ; 1 specimen Willowlake, Mile 88 Richardson Highway, Alaska, 15 February 1964, R. L. Rausch, UN.

From *Lepus townsendi* Bachman, 1859. Oklahoma, USA, no other data, USNM 59076 ; Albany County, Wyoming, USA, R. F. Honess, no other data, USNM 59076.

From *Lepus californicus* Gray, 1837. Idaho, USA, no other data, USNM 59259.
From *Lepus californicus melanotis* Mearns, 1890 ; 12 specimens, Colorado, USA, 1972-1973, P. C. Brittain, D. R. Voth, UN, USNM 74287.

From *Lepus californicus deserticola* Mearns, 1898. 3 specimens, Dugway, Tooele County, Utah, USA, 22 March 1960, A. W. Grundmann, UU 1022 ; 3 specimens, same locality, 14 November 1951,

Source : MNHN, Paris

J. M. Butler, UU 1040 ; 2 specimens, same locality, 21 March 1967, Foster and A. W. Grundmann, UU 1042 ; 2 specimens, Stansbury Is., Great Salt Lake, Utah, USA, March 1960, A. W. Grundmann, UU 8-2.

From *Lepus othus othus* Merriam, 1900. 2 specimens, Nome, Seward Peninsula, Alaska, 1 October 1960, F. H. Fay, Colln. R. L. Rausch.

From *Sylvilagus floridanus* (Allen, 1890). Maryland, USA, no other data, USNM 17449 ; 1 specimen, Bowie, Maryland, USA, A. Hassall, UN (cotype of *Cittotaenia perplexa*).

From *Sylvilagus floridanus mearnsi* (Allen, 1890). 1 specimen, East Lansing, Michigan, USA, 18 April 1946, R. L. Rausch in colln. R. L. Rausch.

From *Sylvilagus nuttalli grangeri* (Allen, 1895). Burch Creek, Montana, USA, no other data, USNM 30957, 30960 ; 14 slides Albany County, Wyoming, USA, R. F. Honess, USNM 59073 ; 3 specimens, 30 miles east of Salina, Utah, USA, 17 May 1957, A. W. Grundmann, UU 157-6.

From *Spermophilus variegatus* (Erxleben, 1777). 4 specimens, Red Canyon, 30 miles east of Salina, Utah, USA, 15 May 1958, A. W. Grundmann, UU 157-1.

Host unknown. Slides of serial sections, Rutshuru, Zaïre, April 1937, J. Ghesquière, UN (described by Mahon, 1954).

? Lepus sp. 1 slide, ? France, collection of R. Blanchard, now in colln. of C. Joyeux, UN.

Description. Large, broad, ribbon-like to small, leaf-shaped worms. Scolex small, rounded, merging imperceptibly into unsegmented neck region of relaxed worms. Neck absent in contracted specimens, scolex difficult to distinguish. Proglottides greatly extended transversely, craspedote. Mature proglottides with approximate length : width- ratio of 1 : 7-1 : 8. Gravid proglottides with ratio 1 : 4-1 : 5. Longitudinal muscle poorly developed, forming two irregular rows of muscle bundles around inner margin of cortex. Inner bundles much smaller and with fewer fibres than outer bundles. Transverse muscle fibres filiform, in band internal to longitudinal muscles. Dorso-ventral muscles fine, single, crossing cortex and medulla at irregular intervals. Longitudinal osmoregulatory canals paired. Ventral canal wider than dorsal canal, situated medially or directly ventrally to it. Transverse canal connects left and right ventral osmoregulatory canals at posterior margin of each proglottis. Numerous accessory canals connect transverse canals of adjacent proglottides. At level of suckers, dorsal canals from each side of strobila join, as do ventral canals. Short dorso-ventral anastomosis connects common dorsal and common ventral duct. Genital atrium of insignificant size, situated in middle of lateral proglottis margin of mature proglottides, dividing margin in ratio 1 : 1 ; situated in posterior third of margin in gravid proglottides dividing margin in ratio 2 : 1. Cirrus sac narrow, elongate, highly variable in size, always reaching lateral nerve, usually reaching or extending beyond longitudinal osmoregulatory canals. Cirrus narrow, frequently coiled, armed with minute bristles. Armature very difficult to detect except in sections. Small, elongate internal seminal vesicle present. Vas deferens narrow, thin-walled, coiled, following course of vagina and seminal receptacle, dividing into two branches at level of vitellarium. Each branch passes transversely dividing into vasa efferentia. External seminal vesicle absent. Testes numerous, entirely posterior to uterus between longitudinal osmoregulatory canals, on dorsal aspect of medulla, in 1-3 transverse and 1-3 horizontal rows. Testes extend beyond female genitalia on both sides of strobila, rarely present directly posterior to vitellarium. Testes between female genitalia usually in unbroken band, sometimes in two separate groups. In some strobilae most mature proglottides have testes in two groups. In other strobilae proglottides with single field or two groups of testes alternate irregulary. Testes persist in near-gravid proglottides. Vagina narrow, lined internally with bristles, surrounded externally by layers of glandular cells. Vagina curves anteriorly and medially with cirrus sac, leads to elongate, thin-walled seminal receptacle without hairy lining or glandular cells. Ovary fan-shaped, composed of numerous clavate lobules, on ventral aspect of medulla. Vitellarium oval or reniform, lobulate, posterior and dorsal to ovary. Mehlis' gland spherical, anterior to vitellarium, dorsal to ovary Uterus tube-like, transverse, usually single, occasionally double. Uterus does not cross longitudinal canals in tubular stage. Lies in middle of proglottis, dorsal to ovary, anterior to Mehlis' gland. Gravid uterus sac-like with numerous anterior and posterior diverticula. Rarely crosses longitudinal osmoregulatory canals, usually displaces

Source : MNHN, Paris

them towards poral margin. Egg spherical with thick refractile shell. Fine sub-shell and inner membranes present. Pyriform apparatus terminating in two elongate horns.

REMARKS. Little can be added to the descriptive anatomy of *M. pectinata* following the detailed accounts by Rees (1933a) and to a lesser extent by Spasskii (1951). However, some minor differences do exist between descriptions. Both Rees (1933a) and Spasskii (1951) considered the cirrus to be unarmed, but, in some whole mounts as well as in serial sections it is possible to distinguish minute bristles. They were not seen on everted cirri and the difficulty in detecting them probably accounts for the earlier descriptions of the cirrus being unarmed. An external seminal vesicle was both described and illustrated by Spasskii (1951). The structure is present only in occasional proglottides and is due simply to dilatation of the distal vas deferens by sperm. In the above description, the external seminal vesicle is stated to be absent.

Measurement are given by many authors for neck length in *M. pectinata*. There is no obvious distinction between the scolex and the neck in this species, though in relaxed specimens there exists an unsegmented region between the posterior margin of the suckers and the first signs of segmentation. The length of this region was used in the present revision as the "neck" length, however, it is of no systematic use because of its dependence on the state of relaxation of the specimen. The anterior end of a type specimen of *Cittotaenia bursaria* von Linstow, 1906 (now a synonym of *M. pectinata*) illustrates (fig. 12) that in a severely contracted specimen, the neck is entirely absent and it is virtually impossible to measure the size of the scolex.

A detailed description of the egg and of the development of the pyriform apparatus was given by Rees (1933b). In one specimen of *M. pectinata* from Canada, irregular cavities were noted in the pyriform apparatus at the base of the arms. (Figs 24, 25).

In spite of a detailed knowledge of the general anatomy of the parasite, considerable deficiencies exist in the information available on variation, particularly in quantitative characters and their bearing on the systematics of the species, as instanced in the discussion below of the various taxa placed as synonyms of *M. pectinata*.

The subspecies of *M. pectinata* have, in the present revision, been supressed. Douthitt (1915), in erecting the sub-species *americana*, drew attention to differences in worm size and proglottis number between it and the European form. Rees (1933a), designating the material she studied from Wales as *C. pectinata europea*, noted several differences from the descriptions of American specimens, namely the smaller scolex, the presence of a neck and the greater length of the strobila, the narrow unbranched dorsal osmoregulatory canal, the greater number of testes and the lack of an external seminal vesicle. Rees (1933a) however did not personally examine American specimens and some of the differences she enumerated are due to errors in early descriptions. Arnold (1938) compared series of the two forms and considered *C. pectinata americana* a valid sub-species though the only consistent differences he gave were those of strobilar size and proglottis number. Both characters are notoriously variable in cestodes, and examination of Table 4 shows that, according to the literature, European specimens may achieve a greater size, but the majority of European specimens examined in the present revision were no bigger and did not contain more proglottides than American specimens. Since all measurements of internal organs also overlap, it is concluded that neither the two subspecies mentioned above, nor *M. pectinata pectinata* Spasskii, 1951, created to replace *C. pectinata europea* as the nominal subspecies, can validly be maintained and they are therefore placed as synonyms of *M. pectinata*.

Cittotaenia wittei Baer and Fain, 1955 was differentiated from *M. pectinata* because of the glandular investment of the vagina and the strongly lobed uterus in the new species. A detailed examination of the types of *C. wittei* revealed no significant differences from *M. pectinata* and it is therefore considered a synonym of the latter species.

Mosgovoyia oitana Sawada and Kugi, 1974 was separated from *M. pectinata* on account of the greater sized scolex, the larger ovary, the position of the genital pores in the posterior half of the lateral proglottis margin and the number of uterine diverticula. The position of the genital pores can vary within a single strobila and can be found in the middle of the lateral proglottis margin in mature proglottides and in the posterior third of gravid proglottides in the same strobila. It is there-

Source : MNHN, Paris

fore not a distinctive character. Comparison of the quantitative data in Table 4 shows that none of the measurements used by Sawada and Kugi (1974) is successful in separating *M. oitana* from *M. pectinata* and hence *M. oitana* falls as a synonym.

M. perplexa (Stiles, 1895) is also regarded as a synonym of *M. pectinata*. Stiles (1896) differentiated *M. perplexa* (then *Cittotaenia perplexa*) by the size of the cirrus sac, the length of the vagina and the fact that in *M. perplexa*, the testes are arranged in two lateral groups in mature proglottides rather than in a single field. Subsequently, Arnold (1938) maintained the validity of *M. perplexa*, differentiating it also on total length, position of appearance in the strobila of the genital primordia and the location of ovarian follicle development. The validity of the two species was also maintained by Honess (1963) working with new collections, though he concluded that the criteria of separation involving length of strobilae and appearance of organ systems were not reliable since they were highly variable or depended upon the technique of preservation. He was, however, able to separate the two species on the features of the scolex and neck.

A re-examination of the range of variability of most of these characters indicates that few are as reliable as has been stated in the past. The features of the scolex and neck region of *M. pectinata* are dependent upon the method of fixation and are extremely variable as shown in figs 11-12. The " width " of the neck cannot be used, as Honess (1963) claimed, to separate the species as its width will depend upon the state of relaxation of the specimen or may be entirely absent. Honess (1963) in fact claimed that Arnold's (1938) drawings of the scolices of *M. pectinata* and *M. perplexa* had been misdesignated as they showed exactly the opposite features to those described by Honess (1963) for the two species. However, Stiles (1896) indicated that the types of *M. perplexa* were contracted and hence Arnold's figure may be taken as correct. The extent of variability seen in specimens of *M. pectinata* in the present review includes both forms used by Honess (1963) to separate the two species.

As stated by Honess (1963), the size of worms and the position of occurrence of genitalia in the strobila were found to be too variable for use as specific characters.

Although in some specimens of *M. perplexa*, the testes are separated into two lateral groups, insufficient emphasis has been placed on the extent of variation in testis distribution. In the types, as noted by Stiles (1896) and Arnold (1938), the testes in immature proglottides form a continuous band across the medulla. They only separate into two groups in mature progfottides. Furthermore, considerable variation may occur within a single strobila. In some of Honess' specimens of *M. perplexa* (USNM no. 59073) proglottides with a single band of testes or with two groups alternate irregularly in the mature region of the strobila. The degree of separation of testes into two groups may vary from the presence of a broad distinct gap to the situation in which the testes in the centre of the proglottis are arranged in a single row with the space of one testis only between the two groups. In Honess' specimens from *Lepus townsendi* from Wyoming determined by him as *M. pectinata* (USNM no. 59076), as well as in specimens from other hosts and localities (USNM nos. 59259, 30098) in which the testes of most progfottides are arranged in a single band, occasional proglottides occur with two groups of testes. A similar situation can occasionally be found in European specimens (BM no. 1693. 7.81). Consequently, as Douthitt (1915) pointed out, the testis distribution is far from invariable and cannot be used successfully to separate *M. pectinata* from *M. perplexa*. Similar variability occurs in other anoplocephlids, particularly in *M. ctenoides (vide infra)*, the genus *Moniezia* (see Theiler, 1924) and in several species of *Progamotaenia* Nybelin, 1917 (see Beveridge, 1976).

The separation of *M. perplexa* and *M. pectinata* on the basis of the size of the cirrus sac appears justifiable from Stiles' measurements of 0.29-0.32 mm and 1.0 mm respectively. Douthitt (1915) remeasured the cirrus sac in the types of *M. perplexa* and found that Stiles was mistaken, the size of the cirrus sac ranging from 0.475-0.640 mm. A difference in cirrus sac size was also found by Arnold (1938) who gave 0.43-0.64 mm and 1.0-1.76 mm for the cirrus sacs of the two species respectivefy. Honess (1963) on the other hand gave measurements of 0.27-0.88 mm and 0.73-1.08 mm respectively, showing overfap between the two groups. If the various sets of measurements are compared with the data obtained from *M. pectinata* in the present study, it is evident that the range 0.43-1.35 mm clearly encompasses the two supposed species, so that the cirrus sac size cannot be used as a distinguishing feature. In the types of both *M. perplexa* and *C. mosaica*, the cirrus sac

Source : MNHN, Paris

reaches the lateral nerve but does not cross the longitudinal osmoregulatory canals (Stiles, 1896, Hall 1908) whilst in *M. pectinata* the cirrus sac crosses the canals (Stiles, 1896). The differences in cirrus sac size and position are certainly quite marked in extreme cases, however Honess (1963) found that whilst the cirrus sac almost invariably crossed the longitudinal osmoregulatory canals in *M. pectinata*, in specimens designated by him as *M. perplexa*, the cirrus sac terminated medial to the canals in 25 % of cases, over the canals in 50 % of cases and lateral to the canals in 25 % of cases. Furthermore, in some specimens examined by the writer, the cirrus sac reached the osmoregulatory canals in mature proglottides, but in gravid proglottides of the same strobilae, did not reach half way to the osmoregulatory canals. The position of the cirrus sac in relation to the osmoregulatory canals therefore shows considerable variability and does not represent a valid distinguishing characteristic. Furthermore, there is no correlation between the occurrence of testes in two groups in a strobila and the size of the cirrus sac. In some of Honess' specimens of *M. pectinata*, the typically long cirrus sac was present in all proglottides but 50 % of the mature proglottides had the testes in two groups.

Each of the morphological features formerly used to separate *M. pectinata* from *M. perplexa* can therefore be shown to vary in such a fashion that neither single nor multiple characters can be used successfully to separate the two. Whilst individual specimens at extremes of the range of variation may be identifiable with one type or the other, all specific parameters overlap and hence *M. perplexa* must fall as a synonym of *M. pectinata*.

Different patterns of variability seem to exist in different parasite populations. In the Wyoming population studied by Honess (1963) a proportion of the cestode population had the morphological characteristics of *M. perplexa*. In other populations, (e.g. from *Lepus americanus* in Alaska, Canada and the U.S.A.) the occurrence of two groups of testes is extremely rare and the cirrus sac is invariably long, extenting beyond the osmoregulatory canals. The causes of this type of variation are unknown but similar observations have been made on populations of *Andrya macrocephala* by Rausch and Schiller (1949) and in *Progamotaenia macropodis* by Beveridge (1976). Voge (1952) retained as valid species *Hymenolepis diminuta* and *H. citelli* solely on the basis of the frequency of occurrence of variations in testis number and position, though she was subsequently able (1969) to support this distinction with biological and fine-structural differences. A comparable study may lead to the re-establishment of *M. perplexa* as a valid taxon, however, the material currently available is insufficient and in the absence of reliable differentiating criteria, *M. perplexa* must fall as a synonym.

It has been possible to establish several cases of mistaken identifications which have appeared in the literature. The cestode reported by Joyeux and Gaud (1945) as *Cittotaenia pectinata* has been re-examined and found to be *C. denticulata*. Joyeux and Baer (1936) also recorded *C. pectinata* from *Oryctolagus cuniculus* in the Carmargue, France, however, the specimens in Joyeux's collection with this collection data are *C. denticulata*.

Edelenyi (1965) reported *C. denticulata* from *Lepus europaeus* in Hungary, however, it is clear from the description and figures that the parasite in question is *M. pectinata*.

Diaz-Ungria and Aleman (1955) described *M. pectinata* from *Sylvilagus floridanus* in Venezuela, however, from the photographs they provide, it appears that the cirrus sac is very small and does not reach halfway to the longitudinal osmoregulatory canals, that the uterus crosses the osmoregulatory canals and that the testes do not extend laterally as far as the canals, all of which are features of *M. variabilis comb. nov.* The photographs also show paired uteri in proglottides, a feature most frequently observed in *M. variabilis* and the host is the usual host of the latter species. Attempts to obtain and examine the material were unsuccessful and for this reason the record is retained provisionally as one of *M. pectinata*.

The present report of *M. pectinata* in *Spermophilus variegatus* represents a new host record. The parasite is only rarely found in hosts other than leporids, though Rankin (1946) recorded it from *Sciurus carolinensis*, a rodent from the same family as *S. variegatus* and Gubanov (1964) has reported it from another sciurid *Citellus undulatus*. In the present case, several specimens were found in the one host by the collector, Dr. A. W. Grundmann, together with *M. variabilis*. Some of the worms were gravid. Although indicating that *M. pectinata* is capable of developing in rodents, the few records available suggest that this is a rare occurrence.

Source : MNHN, Paris

TABLE 4. — MEASUREMENTS OF *MOSGOVOYIA PECTINATA* (in mm)

Author	Stiles (1896)	Stiles (1896)	Lyman (1902)	Linstow (1904)	Hall (1908)	Douthitt (1915)	Douthitt (1915)	Rees (1933)
Parasite described	*C. pectinata*	*C. perplexa*	*M. pectinata*	*C. bursaria*	*C. mosaica*	*C. pectinata americana*	*C. perplexa*	*C. pectinata europea*
Host	*L. timidus* *L. variabilis*	*Syl. florida-nus*	*L. californicus*	*L. nigricollis*	*Syl. pinetis*	*L. californicus*	*Syl. floridanus*	*O. cuniculus*
Length	400	57	44-71		53-100	45		92-320
Width	8	10	7-9		8-10			7.4-10.5
Scolex diameter	0.25	0.32	0.45		0.35	0.70-0.745		0.28
Sucker diameter		0.112	0.120 × 0.088	0.14	0.020 ***			0.10-0.12
					0.044			0.09-0.10
Neck			0	0	0			0.4
No. proglottides			110-140			85		133-322
Mature proglottides				5.0 × 0.2				6.8 × 0.8
Gravid proglottides	10 × 1.5			7.0 × 1.34				10 × 2
Cirrus sac	1.0	0.288 *-0.32	0.925-1.075 × 0.65-0.85	0.44 ** × 0.035	0.475-0.640		0.53	0.83-1.05
No. testes	150		100-125		60-80	100-125		100-202
Testis size	0.64 (?)		0.070-0.092	0.044	0.06-0.09			
Ovary			0.475 × 0.15		0.590-0.645			0.73-0.83
Vitellarium			0.20 × 0.09		0.20-0.23			0.24-0.32
Mehlis' gland			0.09-0.10		0.074-0.092			0.13-0.20
Dorsal osmoregulatory canal			0.034-0.040					01.0-0.13
Ventral osmoregulatory canal			0.034-0.048					
Egg	0.056-0.084		0.050-0.058	0.078	0.067-0.105			
Pyriform apparatus				0.028-0.034				
Oncosphere				0.014				

* Considered an error by Douthitt (1915).
** Remeasured in type — actually 0.87 × 0.09.
*** Measured sucker openings.

Author	Arnold (1938)	Arnold (1938)	Spasskii (1951)	Mahon (1954)	Baer & Fain (1955)	Diaz Ungria & Aleman (1955) ****	Honess (1963)	Honess (1963)	Sawada & Kugi (1974)	Present description
Parasite described	*C. pectinata americana*	*C. perplexa*	*M. pectinata pectinata*	*C. pectinata*	*C. wittei*	*C. pectinata*	*M. pectinata americana*	*M. perplexa*	*M. oitana*	
Host	*L. californicus* *L. americanus*	*Syl. floridanus*		unknown	*L. crawshayi*	*Syl. floridanus*	*L. townsendi*	*Syl. nuttalli*	*L. brachyurus*	
Length	?	70	220		40	17.5-26	240	25-198	250	94-240
Width	7.5	11	12		6.5-7	8-10	11	2.5-11	10-15	7-11
Scolex diameter	0.23-0.30	0.32-0.45	0.3		0.45	0.60-0.93	0.23-0.65	0.22-0.481	0.49-0.52	0.15-0.65
Sucker diameter	0.11-0.17	0.11	0.13		0.13	0.215-0.260			0.11-0.12	0.12-0.15
	0.14-0.30	0.30-0.35	0.12				0.14-0.30		0.21-0.27	0-0.3
Neck	360	150				380-400	372	106-270		156-372
No. proglottides			4-7 × 0.3-0.4							3.9-4.2 × 0.5-0.6
Mature proglottides										5.5-11.0 × 1.3-1.5
Gravid proglottides			8.9 × 1.5							
Cirrus sac	1.0-1.76	0.43-0.50	0.8-1.2	0.6-1.1	0.6-0.9	0.27-0.39	0.72-1.76	0.27-0.88	0.48-0.55	0.43-1.76 × 0.05-0.07
No. testes	112-125	120-125	200	120-150	80-100	125-160	63-125	42-118	80-100	63-179
Testis size	0.062-0.11	0.049-0.065	0.07-0.08			0.060-0.090	0.05-0.115	0.05-0.11	0.083-0.097	0.04-0.12
Ovary										
Vitellarium										
Mehlis' gland										
Dorsal osmoregulatory canal	0.6	0.50-0.61	0.21 × 0.15		0.45-0.55		0.52-0.99	0.26-0.63	1.11-1.25	0.35-1.1 × 0.23-0.45
Ventral osmoregulatory canal			0.11		0.20				0.42-0.50	0.11-0.3 × 0.07-0.20
Egg										0.1
Pyriform apparatus										0.04
Oncosphere	0.07-0.13	0.057-0.069	0.07-0.086		0.072-0.07	0.072-0.078			0.077-0.084	0.07
					0.012-0.013				0.018-0.021	

**** The species is probably *M. variabilis*.

Source : MNHN, Paris

TABLE 5. — HOST RECORDS OF *MOSGOVOYIA PECTINATA*

Host	Locality	Original Determination	Reference
Oryctolagus cuniculus Linnaeus, 1785			
	Great Britain	*C. pectinata*	Mead-Briggs and Page (1975)
	Surrey, England	*C. pectinata*	Mead-Briggs and Vaughan (1973)
	England, Wales	*C. pectinata*	Baylis (1939)
	Aberystwyth, Wales	*C. pectinata*	Rees (1933a), Evans (1940)
	Scotland	*C. pectinata*	Cameron and Parnell (1933) Fahmy (1960)
	I. of Eigg, Scotland	*C. pectinata*	Mackintosh (1955)
	I. de St. Pierre, Switzerland	*M. pectinata*	Hörning (1974)
	Granada, Spain	*C. pectinata*	López-Neyra (1947)
	USSR	*M. pectinata*	Gvozdev *et al.* (1970)
	Richelieu, France	? *C. pectinata*	Dollfus (1961)
	France	*C. pectinata*	Joyeux and Baer (1936)
	Czechoslovakia (Zoo)	*M. pectinata*	Jaros *et al.* (1966)
Lepus europaeus Pallas, 1778			
	Great Britain *	*C. pectinata*	Mead-Briggs and Page (1975)
	England	*C. pectinata*	Irvin (1970)
	Sweden	*C. pectinata*	Burgaz (1970)
	Lorraine, France	*C. pectinata*	Joyeux and Baer (1936)
	Travers, Switzerland	*C. pectinata*	Bouvier (1965)
	Poland	*M. pectinata*	Drygas and Piotrowski (1955)
	Poznam, Poland	*M. pectinata*	Czaplińksi *et al* (1965)
	Bialystock, Poland	*M. pectinata*	Wieczorowski (1968)
	Hungary	*C. denticulata*	Edelényi (1965)
	Bulgaria	*M. pectinata*	Yanchev (1963a, b, 1970, 1973)
	Azerbaidjan USSR	*M. pectinata*	Sadikhov (1958)
	Ukraine, USSR	*M. pectinata*	Sharpilo (1966)
	Georgia, USSR	*M. pectinata*	Rodonaya (1967)
	Gruzia, USSR	*M. pectinata*	Rodonaya (1966)
	Northern Caucasus, USSR	*C. pectinata*	Naumov (1944)
	USSR	*M. pectinata*	Gvozdev *et al.* (1970)
	Azerbaidjan, USSR	*M. pectinata*	Sadikhov (1962)
	Byelorussia, USSR	*M. pectinata*	Merkusheva (1960)
Lepus europaeus crawshayi de Winton, 1899 (syn. *Lepus crawshayi* de Winton, 1899)			
	Zaïre	*C. wittei*	Baer and Fain (1955)
Lepus europaeus saxatilis Cuvier, 1823 (syn. *Lepus saxatilis* Cuvier, 1823)			
	Mozambique	*M. pectinata*	Cruz E. Silva (1971)

* Host originally given as *L. capensis occidentalis*, a change in host nomenclature having taken place since 1951.

Source : MNHN, Paris

Host	Locality	Original Determination	Reference
Lepus capensis Linnaeus, 1758			
	Afghanistan	*M. pectinata*	Tenora and Kullmann (1970)
Lepus capensis granatensis Rosenhauer, 1856 (syn. *Lepus granatensis* Rosenhauer, 1856)			
	Granada, Spain	*C. pectinata*	López-Neyra (1947)
Lepus capensis tibetanus Waterhouse, 1841 (syn. *Lepus tibetanus* Waterhouse, 1841)			
	Kazakstan, USSR	*C. pectinata*	Gvozdev (1948)
Lepus capensis talai Pallas, 1778. (syn. *Lepus tolai* Pallas, 1778)			
	Bartoga, USSR	*M. pectinata*	Gvozdev (1965)
	Kirgizia, USSR	*M. pectinata*	Tokobaev (1960) Tokobaev and Erkulov (1966)
	USSR	*M. pectinata*	Gvozdev *et al.* (1970)
	Kazakhstan, USSR	*M. pectinata*	Gvozdev (1964)
	Tadzhikistan, USSR	*M. pectinata*	Gafurov *et al.* (1971)
Lepus timidus Linnaeus, 1758 (syn. *Lepus variabilis* Pallas, 1778)			
	Briançon, France	*C. pectinata*	Stiles (1896), Joyeux and Baer (1936)
	Sweden	*C. pectinata*	Burgaz (1970)
	Scotland	*C. pectinata*	Irvin (1970)
	Germany	*C. pectinata*	Stiles (1896)
	Verkhoyansk, USSR	*M. pectinata*	Gubanov and Federov (1956)
	Yakutia, USSR	*M. pectinata*	Gubanov *et al.* (1957)
	USSR	*C. pectinata*	Naumov (1940)
	Vaud, Switzerland	*Ct. pectinata*	Galli-Valerio (1909, 1930a)
	Tobolk, USSR	*C. pectinata*	Romanovitch (1915)
	Yakutia, USSR	*M. pectinata*	Gubanov (1964)
	Kirov, USSR	*C. pectinata*	Naumov (1944)
	Buriat, USSR	*M. pectinata*	Oshmarin (1965)
	Moscow, USSR	*M. pectinata*	Maklakova (1973)
	Azerbaidjan, USSR	*M. pectinata*	Sadikhov (1962)
	Byelorussia, USSR	*M. pectinata*	Merkusheva (1960)
Lepus brachyurus Temmink, 1845			
	Kyushu, Japan	*M. oitana*	Sawada and Kugi (1974)
	USSR	*M. pectinata*	Gvozdev *et al.* (1970)
	Tohoku, Japan	*M. pectinata*	Inaba and Yagisawa (1973)
Lepus timidus scotius Hilzheimer			
	Great Britian	*C. pectinata*	Mead-Briggs and Page (1975)
Lepus nigricollis Cuvier, 1823			
	Sri Lanka	*C. bursaria*	von Linstow (1906)
	India	*C. pectinata*	Southwell (1930)

Source : MNHN, Paris

Host	Locality	Original Determination	Reference
Lepus nigricollis ruficaudatus Geoffroy, 1826 (syn. *Lepus ruficaudatus* Geoffroy, 1826)			
	India	*C. pectinata*	Southwell (1930)
	India	*C. pectinata*	Katiyar and Pande (1965)
Lepus americanus Erxleben, 1777			
	Manitoba, Canada	*C. pectinata*	Boughton (1932)
	Alaska, USA	*C. p. americana*	Philip (1937, 1948)
	Wyoming, USA	*M. pectinata*	Honess (1963)
	Minnesota, USA	*C. pectinata*	Erikson (1944)
Lepus americanus struthopus Bangs, 1898			
	Newfoundland, Canada	*M. pectinata*	Dodds and Mackiewicz (1961)
Lepus californicus Gray, 1837			
	New Mexico, USA	*M. pectinata*	Samson (1968)
	California, USA	*C. pectinata*	Lechleitner (1959)
Lepus californicus melanotis Mearns, 1890			
	Kansas, Nebraska, USA	*C. pectinata*	Lyman (1902), Douthitt (1915), Arnold (1938)
	Colorado, USA	*C. pectinata*	Brittain and Voth (1975)
Lepus californicus deserticola Mearns, 1898			
	Utah, USA	*C. p. americana*	Grundmann (1958)
Lepus townsendi campanius Hollister, 1915			
	North Dakota, USA	*C. ? pectinata*	Voth and James (1965)
	Wyoming, USA	*M. p. americana*	Honess and Winter (1956)
* *Caprolagus hispidus* (Pearson, 1839) (syn. *Lepus hispidus* Pearson, 1839)			
	India	*C. pectinata*	Southwell (1930)
Sylvilagus floridanus Allen, 1890			
	North Dakota, USA	*M. p. americana*	Novlesky and Dyer (1970)
	Eastern USA	*C. perplexa*	Bell and Chalgren (1943)
	Oklahoma, USA	*C. perplexa*	Douthitt (1915)
	Maryland, USA	*C. perplexa*	Stiles (1896)
Sylvilagus floridanus mallurus Thomas, 1898			
	North Carolina, USA	*C. pectinata*	Harkema (1936)
Sylvilagus floridanus mearnsii Allen, 1894			
	Minnesota, USA	*C. pectinota*, *C. perplexa*	Erikson (1947)
	Michigan, USA	*C. pectinata*	Haugen (1942)

* Host identification uncertain.

Source : MNHN, Paris

Host	Locality	Original Determination	Reference
Sylvilagus floridanus margarita Miller, 1898			
	Venezuela	*C. pectinata* (determination doubtful)	Díaz-Ungría and Aleman (1955)
Sylvilagus floridanus alacer Bangs, 1896			
	USA	*M. p. americana*, *M. perplexa*	Honess and Winter (1956)
Sylvilagus nuttalli grangeri Allen, 1895			
	Wyoming, USA	*C. pectinata*, *C. perplexa*	Honess (1935)
		M. p. americano, *M. perplexa*	Honess and Winter (1956)
Sylvilagus nuttalli pinetis Allen, 1894			
	Colorado, USA	*C. mosaica*	Hall (1908)
	Wyoming, USA	*M. perplexa*	Honess and Winter (1956)
Sciurus carolinensis pennsylvanicus Ord, 1815 (syn. *Sciurus leucotis* Gapper, 1830)			
	Massachusetts, USA	*C. p. americana*	Rankin (1946)
Citellus undulatus Pallas, 1778			
	Yakutia, USSR	*M. pectinata*	Gubanov (1964)

Mosgovoyia ctenoides (Railliet, 1890) comb. nov.
Figs 26-34. Tables 6-7.

Dipylidium leuckarti Riehm, 1881a : 200, 566-577, pl. 5, figs 3, 11-13, 16, pl. 6, figs 5-6.
Taenia leuckarti (Riehm, 1881) Neumann, 1888 : 426.
Moniezia leuckarti (Riehm, 1881) Blanchard, 1891 : 187, 444, 450-451.
Ctenotaenia leuckarti (Riehm, 1881) Railliet, 1893, : 278.
Cittotaenia leuckarti (Riehm, 1881) Stiles and Hassall, 1896b : 407.
Taenia ctenoides Railliet, 1890 : 346.
Cittotaenia ctenoides (Railliet, 1890) Stiles 1896 : 179-181, pl. 14.
Ctenotaenia ctenoides (Railliet, 1890) Spasskii, 1951 : 268-269. fig. 125.
Neoctenotaenia ctenoides (Railliet, 1890) Tenora, 1976 : 13.

TYPES. From *Oryctolagus cuniculus* Linnaeus, 1758, Germany, coll. Riehm, cotype in USNM 1327.

MATERIAL EXAMINED.

From *Oryctolagus cuniculus* Linnaeus, 1758. 2 specimens, Milford, Surrey, England, 8 August, 1974, A. Mead-Briggs, UMVS ; 10 slides, Paris, France, 5 February 1921, 1930, C. Joyeux, UN ; 1 spe-

Source : MNHN, Paris

cimen, St. Quentin, France, 17 December 1929, C. Joyeux, UN ; 3 specimens, Algeria, 1 November 1926, C. Joyeux, UN ; 2 specimens, Ile de St. Pierre, Switzerland, 17 March 1976, B. Hörning, UN ; 3 specimens, Graz, Austria, June 1976, E. Ebermann, in colln. of E. Ebermann.

Description. Large, broad, ribbon-like worms. Scolex small, rounded anteriorly, merging imperceptibly into neck region or may be demarcated from neck by slight constriction posterior to suckers. Proglottides craspedote, extended transversely. Mature proglottides with approximate length : width ratio of 1 : 4-1 : 6. Gravid proglottides with similar ratio. Longitudinal musculature weakly developed, arranged in two rows of muscle bundles. Bundles of inner row smaller with up to 25 fibres per bundle. Bundles of outer row larger, elongate with more fibres. Transverse muscle fibres fine, arranged in band internal to longitudinal muscles. Dorso-ventral muscles weakly developed, composed of individual, irregularly arranged fibres. Longitudinal osmoregulatory canals paired. Ventral canal straight, thin-walled, wider than dorsal canal. Dorsal canal narrow, surrounded by layer of muscle cells. Transverse canal connects left and right ventral canals at posterior margin of each proglottis. Dorsal canals from each side join one another at level of suckers, similarly ventral canals fuse. Short common dorsoventral duct joins the fused canals from each side. Accessory canals connecting adjacent transverse canals in strobila absent. Genital atrium of insignificant size, situated in posterior half of lateral proglottis margin, dividing margin in ratio 1 : 2-1 : 3. Cirrus sac very short, ellipsoidal, never reaching more than halfway from lateral proglottis margin to longitudinal osmoregulatory canals. Cirrus short, coiled, unarmed. Internal seminal vesicle present occupying up to two-thirds of volume of cirrus sac. Vas deferens thin-walled, coiled, follows course of vagina and seminal receptacle to vicinity of Mehlis' gland and divides into numerous vasa efferentia. Testes numerous, in 2-4 transverse and 1-5 horizontal rows entirely posterior to uterus. Testes densest just to aporal side of ovaries, some overlying lobules of ovary dorsally. Testes extend posterior to vitellarium, with 3-8 testes poral to females genitalia. Testes usually in two lateral groups with median space, number of testes towards centre of proglottis low. Occasionally testes form continuous band across medulla. Both types of arrangement of testes may occur within one strobila. Testes do not persist in gravid proglottides. Vagina narrow, surrounded externally by layers of glandular cells. Vagina terminates near longitudinal osmoregulatory canals in narrow duct without surrounding glandular cells which leads into elongate, thin-walled seminal receptacle, also without glandular cells. Seminal receptacle terminates in narrow duct in vicinity of Mehlis' gland. Ovary fan-shaped, composed of numerous clavate lobules, situated on ventral aspect of medulla. Vitellarium reniform, lobulate, posterior and dorsal to ovary. Mehlis' gland spherical, anterior and dorsal to vitellarium. Uterus tube-like, transverse, usually single, occasionally paired, extending across middle of medulla anterior to Mehlis' gland. Poral to Mehlis' gland, uterus bends posteriorly, crosses longitudinal osmoregulatory canals dorsally and terminates posterior to vagina and proximal extremity of cirrus sac. Gravid uterus with numerous anterior and posterior diverticula. Egg spherical, shell thick, refractile, subshell and inner membranes present. Pyriform apparatus drawn into two elongate horns.

Remarks. The above description of *M. ctenoides* is similar in most respects to that of earlier publications. It agrees with Dollfus' description (1951) in that the testis distribution is somewhat variable and that the testes may be distributed in a single band or in two groups posterior to the uterus. Dollfus' suggestion that the size and morphology of the cirrus sac are more reliable taxonomic characters than testis distribution is also confirmed, though it is considered safest to use the fact that the cirrus sac never reaches more than half way to the longitudinal osmoregulatory canals rather than the absolute size of the cirrus sac which might vary between worms. *M. ctenoides* is readily distinguished from *M. pectinata*, the species most closely related to it by the form of the cirrus sac and by the fact that in *M. ctenoides* the uterus invariably extends beyond the osmoregulatory canals even in the early stages of its development. This species is distinguishable from *M. variabilis* by the shape of the cirrus sac and by the occurrence of testes poral to the female genitalia in *M. ctenoides* but not in *M. variabilis*.

Riehm (1881a) described a branched osmoregulatory system in the posterior proglottides of this species, and his figure was subsequently reproduced by Stiles (1896) and Spasskii (1951). This

Source : MNHN, Paris

type of system is not found in strobilae which are apolytic and is probably an abnormality which may occur in the first formed proglottides of a strobila.

The descriptions of the egg and pyriform apparatus are similar to those of Obitz (1934).

Several authors have recorded this species from north American leporids (see Table 7). Unfortunately their specimens could not be located and the occurrence of this species has not been confirmed in the material to hand from North America.

Although the specific epithet commonly used since the revision of Stiles (1896) has been *ctenoides*, recently, Dollfus (1951) and Yamaguti (1959) have revived the use of the earlier epithet *leuckarti*, both without any explanation of its use. The species was first described under the name *Dipylidium leuckarti* by Riehm (1881a), and as Stiles (1896) has shown, the original description is quite adequate and cannot be confused with other species. Railliet (1890) described the same parasite under the name *Taenia ctenoides*, but subsequently (1893) recognised the synonymy of the two and treated *T. ctenoides* as a synonym placing *D. leuckarti* in his new genus *Ctenotaenia*. The specific name was also recognised as *leuckarti* by Stiles and Hassall (1896b) in their paper on the priority of the genus *Cittotaenia* over *Ctenotaenia* in which they established the new combination *Cittotaenia leuckarti*. Stiles (1896) however introduced the combination *Cittotaenia ctenoides* without any explanation and this name has persisted in common use. The probable reason for this change was Stiles' discovery that in 1888, Neumann had proposed the name *Taenia leuckarti*, apparently unaware that the name was preoccupied by *Taenia leuckarti* Krabbe, 1869. The name under these circumstances was probably presumed lost by Stiles and the name first applied to the parasite after Neumann's error, that of *Taenia ctenoides* was taken as the correct name. However, if one applies current rules of zoological nomenclature (Art. 59 and ammendments of 1972) then Blanchard's removal of the species under the combination *Moniezia leuckarti* ensures the survival of the specific epithet *leuckarti*. According to current amendments, since Neumann's transfer of the species and the resulting homonomy were overlooked prior to Stiles' (1896) revision, Blanchard's (1891) transfer of the species to the genus *Moniezia* means that *leuckarti* is the correct current epithet. However, at the time of Stiles' work, the code of nomenclature did not exist as such, and since Stiles' action is quite logical and probably follows usage of that period, the question of the correctness of the specific epithet would appear to hinge upon whether one considers the rules of nomenclature can be made retrospective to decisions taken before their existence.

Furthermore, as mentioned earlier, the name *ctenoides* has been in common use since 1896 and except for a paper by Smith in 1908, and those of Dollfus (1951) and Yamaguti (1959), the name *leuckarti* has not been used. Although *leuckarti* cannot be considered a *nomen oblitum* because not 50 years has elapsed since its use, it is virtually such in practice. In the present review, it has been decided to allow common use to prevail and to continue to use the epithet *ctenoides*. A formal submission will be made to the International Commission of Zoological Nomenclature on the correct name.

TABLE 6. — MEASUREMENTS OF *MOSGOVOYIA CTENOIDES* (in mm)

Host	Stiles (1896) *O. cuniculus*	Arnold (1938) *O. cuniculus*	López-Neyra (1947) *O. cuniculus*	Dollfus (1951) *O. cuniculus*	Present description *O. cuniculus*
Length	800	460	200-300	430-550	173-243
Width	10	10.5	7-7.5	7-10	10-14
Scolex diam.		0.32-.048	0.45-.046		0.30-0.52
Sucker diam.	0.176	0.12-0.25	0.11-0.164	0.14-0.162	0.12-0.22
Neck		0.25-0.42			0.38-0.65
No. proglottides		560	300		410-510
Mature proglottides					3.5-5.5 × 0.75-1.0

Source : MNHN, Paris

Host	Stiles (1896) *O. cuniculus*	Arnold (1938) *O. cuniculus*	López-Neyra (1947) *O. cuniculus*	Dollfus (1951) *O. cuniculus*	Present description *O. cuniculus*
Gravid proglottides					4.5-8.3 × 1.5-1.7
Cirrus sac	0.16 × 0.128	0.15-0.25	0.29 × 0.13	0.12-0.7 × 0.065-0.128	0.16-0.25 × 0.08-0.12
Internal seminal vesicle					0.1-0.16 × 0.06-0.08
No. testes	120-160	70-150		50-70	100-160
Testis size	0.05-0.06	0.046-0.081		0.05-0.07	0.04-0.07
Ovary		0.40-0.88			0.45-0.55 × 0.35-0.50
Vitellarium					0.15-0.3 × 0.08-0.18
Mehlis'gland					0.12
Dorsal osmoregulatory canal					0.015
Ventral osmoregulatory canal					0.07
Egg	0.064	0.062-0.069	0.07-0.085	0.056	0.06-0.07
Pyriform apparatus					
Oncosphere					

TABLE 7. — HOST RECORDS OF *MOSGOVOYIA CTENOIDES*

Host	Locality	Original Determination	Reference
Oryctolagus cuniculus Linnaeus, 1785			
	Great Britain	*C. ctenoides*	Mead-Briggs and Page (1975)
	Surrey, England	*C. ctenoides*	Mead-Briggs and Vaughan (1973)
	Wales	*C. ctenoides*	Stephens (1952)
	Netherlands	*C. ctenoides*	van der Broek and Jansen (1964)
	France	*C. ctenoides*	Stiles (1896)
	Paris, Toulouse, St. Quentin, France	*C. ctenoides*	Joyeux and Baer (1936)
	Rhiems, France	*C. ctenoides*	Courtehoux (1948)
	Richelieu, Cadarache, France	*C. leuckarti*	Dollfus (1951, 1961)
	Germany	*C. ctenoides*	Stiles (1896)
	Hamburg, Germany	*C. ctenoides*	Arnold (1938)
	Czechoslovakia	*Ct. ctenoides*	Pačenovsky (1973)

Source : MNHN, Paris

Host	Locality	Original Determination	Reference
	Granada, Spain	*C. ctenoides*	López-Neyra (1947)
	Huesca, Spain	*C. ctenoides*	Tarazona Vilas (1955)
	Portugal	*C. ctenoides*	da Silva Leitão (1964)
	Morocco	*C. leuckarti*	Dollfus (1951)
	Algeria	*C. ctenoides*	Joyeux (1927)
	Azores	*C. ctenoides*	Stiles (1896)
? *Lepus europaeus* Pallas, 1778			
	Czechoslovakia	*Ct. ctenoides*	Novak *et al.*, (1966)
Lepus californicus Gray, 1837			
	Oklahoma, USA	*C. ctenoides*	Ward (1934)
Sylvilagus floridanus Allen, 1890			
	North Dakota, USA	*C. ctenoides*	Novlesky and Dyer (1970)
	Oklahoma, USA	*C. ctenoides*	Ward (1934)
	Philadelphia, USA	*Ct. leuckarti*	Smith (1908)
Sylvilagus floridanus alacer Bangs, 1896			
	Oklahoma, USA	*C. ctenoides*	Smith (1940)
Sylvilagus aquaticus Bachman, 1837			
	Oklahoma, USA	*C. ctenoides*	Ward (1934)
Sylvilagus aquaticus aquaticus Bachman, 1837			
	Oklahoma, USA	*C. ctenoides*	Smith (1940)

Mosgovoyia variabilis (Stiles, 1895) comb. nov.
Figs 35-40, Tables 8, 9.

Ctenotaenia variabilis Stiles, 1895 : 345.
Cittotaenia variabilis (Stiles, 1895) Stiles and Hassall, 1896b : 407.
Cittotaenia variabilis angusta Stiles, 1896 : 193, pl. 19, figs 13-14.
Cittotaenia variabilis imbricata Stiles, 1896 : 193.
Neoctenotaenia variabilis (Stiles, 1895) Tenora, 1976 : 13.
Cittotaenia pectinata (Goeze, 1782) *pro parte* Baer, 1927 : 55.

Types. From *Sylvilagus floridanus* (Allen, 1890). (syn. *Lepus sylvestris* Allen, 1890), Bowie, Maryland, USA, A. Hassall, USNM, BM 95.9.11.1. For details see Stiles (1896).

Material examined.

From *Sylvilagus floridanus* (Allen, 1890). 1 specimen, New York, USA, C. Bursey, UN ; 3 specimens, Lincoln, Nebraska, USA, 4 October 1897, A. S. Pearse, from collection of H. B. Ward, UN ; 1 specimen, cotype, Bowie, Maryland, USA, A. Hassall, BM 95.9.11.1 ; 1 specimen, Colorado, USA, G. D. Schmidt, in colln. of G. D. Schmidt.

Source : MNHN, Paris

From *Sylvilagus floridanus mearnsi* (Allen, 1894). 1 specimen, East Lansing, Michigan, USA, 29 November, 1945, R. L. Rausch, in colln. R. L. Rausch.

From *Sylvilagus nuttalli grangeri* (Allen, 1895). 1 specimen, Curacanti Res., Gunnison River, Colorado, USA, 2 July 1961, A. W. Grundmann, UU 49; Wyoming, USA, no other data, USNM 59078; Montana, USA, no other data, USNM 30954.

From *Sylvilagus palustris* Bachman, 1837. Georgia, USA, no other data, USNM 30954.

From *Sylvilagus* sp. Virginia, USA, USNM 39887; Louisiana, USA, USNM 28513.

From *Oryctolagus cuniculus* Linnaeus, 1758 dom. 1 specimen, Ohio, 1943-1944, R. Rausch, in coll. of R. Rausch; 1 specimen, Coshocton, Ohio, 28 November 1944, R. Rausch, in coll. of R. Rausch.

From *Spermophilus variegatus* (Erxleben, 1777). 2 specimens, Red Canyon, 30 miles east of Salina, Utah, USA, 15 May 1958, A. W. Grundmann, UU 157-1.

Description. Large broad ribbon-like worms. Scolex small, rounded anteriorly merging imperceptibly into neck region, or in some specimens subglobular, distinctly demarcated from strobila with neck absent. Proglottides craspedote, greatly extended transversely. Mature proglottides with approximate length : width ratio of 1 : 6. Gravid proglottides with ratio of 1 : 8. Longitudinal musculature weakly developed, arranged in two rows of bundles around inner edge of cortex. Transverse muscles fine, arranged in band internal to longitudinal muscles. Dorso-ventral muscles fine, few in number, irregularly arranged. Longitudinal osmoregulatory canals paired. Dorsal canal narrow, surrounded by layer of muscle cells, medial to ventral canal. Ventral canal wider, thin-walled. Transverse canal connects left and right osmoregulatory canals at posterior margin of each proglottis. Accessory canals connecting transverse canals absent. Dorsal canals from each side of strobila join in midline at level of suckers. Common duct passes anteriorly fusing with common ventral duct by short dorso-ventral anastomosis. Genital atrium of insignificant size, situated in anterior half of lateral proglottis margin, dividing margin in ratio 5 : 4. Cirrus sac small, elongate, thin-walled, reaching only half way to longitudinal osmoregulatory vessels. Cirrus straight, unarmed. Small, elongate internal seminal vesicle present. Vas deferens narrow, thin-walled, coiled, following course of vagina and seminal receptacle, decreasing in diameter. Vasa efferentia not seen. Testes numerous almost invariably situated in single transverse band, always posterior to uterus, on dorsal aspect of medulla, between female genitalia. Rarely testes in single proglottis almost separated into two groups. Laterally, testes extend no further than aporal margin of vitellarium. Testes in 2-4 horizontal and 1-2 transverse rows. Testes do not persist in gravid proglottides. Vagina narrow, surrounded by layers of glandular cells. Two thirds of distance to osmoregulatory canals, vagina leads into narrow thin-walled duct without surrounding glandular cells. Duct extends medially to elongate, thin-walled seminal receptacle dorsal to ovary. Ovary fan-shaped, composed of numerous clavate lobules, situated on ventral aspect of medulla. Vitellarium reniform, lobulate, posterior and dorsal to ovary. Mehlis' gland spherical, anterior to vitellarium, dorsal to ovary. Uterus paired or single, transverse extending across middle of proglottis anterior to Mehlis'gland, dorsal to ovary. Uterus passes posteriorly, crosses longitudinal osmoregulatory canals dorsally, terminating posterior to vagina and cirrus sac. Paired uteri may meet in midline or there may be additional small cavities between uteri, lined with squamous epithelium rather than with cuboidal epithelium of uteri. Gravid uterus sac-like, without prominent diverticula. Egg spherical, thick-shelled. Thick sub-shell membrane and very fine inner membrane present. Oncosphere surrounded by pyriform apparatus, latter forming two elongate horns.

Remarks. Some confusion exists in the literature between this species and *M. pectinata* probably due to Baer's (1927) earlier attempt to synonymise the two. The two species differ markedly in the extension of the uterus of *M. variabilis* across the osmoregulatory canals in the tubular stage, the uterus of *M. pectinata* being at all times restricted to the cortex, and in the distribution of testes which lie between the female genitalia in *M. variabilis* but extend lateral to the female genitalia in *M. pectinata*. *M. variabilis* possesses in common with *M. ctenoides* a muscular coat to the dorsal osmoregulatory canal which is absent in *M. pectinata*. *M. variabilis* can be distinguished from *M. ctenoides*

Source : MNHN, Paris

by the shape of the cirrus sac and by the distribution of the testes. Although the testes in *M. variabilis* are nearly always distributed in a single band, occasional proglottides can be found in which two groups are present indicating similar patterns in variability of testis distribution to *M. pectinata* and *M. ctenoides*.

Lyman (1902) described a sphincter surrounding the genital atrium in this species but his observations have not since been confirmed and no such sphincter was seen in the material currently available.

This species is virtually restricted to host species belonging to the genus *Sylvilagus*, apart from the single record included here from the rodent *Spermophilus variegatus*, and from the domestic rabbit, *Oryctolagus cuniculus*.

TABLE 8. — MEASUREMENTS OF *MOSGOVOYIA VARIABILIS* (in mm)

	Stiles (1896) *Sylvilagus floridanus* (*L. sylvaticus L. palustris*)	Lyman (1902) *Syl. floridanus* (*L. sylvaticus*)	Arnold (1938) *Sylvilagus floridanus*	Houess (1963) *Sylvilagus nuttalli*	Present description
Length	100-180	170-180	450	111-324	104-940
Width	10		10.5	3-8	8-14
Scolex diam.	0.32-0.56	0.462-0.872	0.44-0.61	0.37-078	0.48-0.75
Sucker diam.	0.11-0.28 × 0.11-0.24	0.2-0.282 × 0.106	0.16-0.28		0.20-0.26
Neck			0.26-0.84		0-0.4
No. proglottides			750	313-519	340-660
Mature proglottides					4.0-6.9 × 0.55-1.0
Gravid proglottides					5.5-7.5 × 0.55-1.0
Cirrus sac		0.4 × 0.05	0.32-0.45		0.25-0.70 × 0.04-0.05
No. testes	65-90	75-100	60-135		80-120
Testis size		0.08-0.10	0.053-0.071		0.07-0.08
Ovary		0.69 × 0.1	0.48-0.71		0.4-0.6 × 0.2-0.5
Vitellarium		0.266 × 0.088			0.15-0.22 × 0.13-0.18
Mehlis' gland					0.09-0.13
Dorsal osmoregulatory canal					0.005-0.03
Ventral osmoregulatory canal					0.1-0.25
Egg	0.06-0.064	0.058	0.052-0.068		0.045
Pyriform apparatus	0.012-0.016	0.016			0.030
Oncosphere					0.015

Source : MNHN, Paris

TABLE 9. — HOST RECORDS OF *MOSGOVOYIA VARIABILIS*

Host	Locality	Original determination	Reference
Sylvilagus floridanus (Allen, 1890)			
	North Dakota, USA	*Ct. variabilis*	Novlesky and Dyer (1970)
	North Carolina, USA	*C. variabilis*	Stringer *et al.* (1969)
	Eastern USA	*C. variabilis*	Bell and Chalgren (1943)
	Maryland, Long Is., USA	*C. variabilis*	Stiles (1896)
	Nebraska Kansas, USA	*C. variabilis*	Lyman (1902)
	Alabama, USA	*C. variabilis*	Price and Ingram (1959)
Sylvilagus floridanus alacer (Bangs, 1896)			
	Kansas, USA	*C. variabilis*	Arnold (1938)
Sylvilagus floridanus mallurus (Thomas, 1898)			
	Alabama, USA	*C. variabilis*	Moore and Moore (1947)
	Connecticut, USA	*C. variabilis*	Clancy *et al.* (1940) Hosley (1942)
	New York, Pennsylvania, USA	*C. variabilis*	Arnold (1938)
	Alabama, USA	*C. variabilis*	Moore (1939)
Sylvilagus floridanus mearnsii (Allen, 1894)			
	Minnesota, USA	*C. variabilis*	Erikson (1947)
	Iowa, USA	*C. variabilis*	Morgan and Waller (1940)
Sylvilagus transitionalis (Bangs, 1895)			
	Massachusets, USA	*C. variabilis*	Rankin (1946)
	Connecticut, USA	*C. variabilis*	Clancy *et al.* (1940) Hosley (1942)
Sylvilagus auduboni (Baird, 1858)			
	Colorado, USA	*C. variabilis*	McCrease (1957)
Sylvilagus auduboni vallicola Nelson, 1907			
	California, USA	*C. ? variabilis*	Herman and Jankiewicz (1943)
Sylvilagus nuttalli grangeri (Allen, 1895)			
	Wyoming, USA	*C. variabilis*	Honess (1935)
		Ct. variabilis	Honess and Winter (1956)
Sylvilagus nuttalli pinetis (Allen, 1894)			
	Colorado, USA	*C. variabilis*	Stock (1962)
Sylvilagus palustris Bachman, 1837			
	North Carolina, USA	*C. variabilis*	Stringer *et al.* (1969)
	Florida USA	*C. variabilis*	Stiles (1896)
	? Maryland, USA	*C. variabilis*	Arnold (1938)
Lepus americanus (Erxleben, 1777)			
	Minnestoa, USA	*C. variabilis*	Erikson (1944)

Source : MNHN, Paris

Genus *PSEUDOCITTOTAENIA* Tenora, 1976 *emend.*

Pseudocittotaenia Tenora, 1976 : 14-15.

Types Species. *Pseudocittotaenia praecoquis* (Stiles, 1895).

Diagnosis. Small cestodes. Scolex rounded, unarmed. Suckers unarmed. Proglottides numerous (over 50 in gravid strobilae), craspedote, extended transversely. Longitudinal osmoregulatory canals paired. Transverse canal connects left and right ventral canals at posterior margin of each proglottis. Genital ducts cross longitudinal osmoregulatory canals dorsally. Genitalia paired. Cirrus sac opens to genital atrium anterior to vagina. Cirrus sac dorsal to vagina on both sides of strobila. Internal seminal vesicle present. External seminal vesicle present or absent. Testes numerous, entirely posterior to uterus, either restricted to area between female genitalia or extending laterally to female genitalia. Seminal receptacle large, prominent. Ovaries situated in lateral quarters of proglottis medulla. Single transverse, tubular uterus in each proglottis at anterior extremity of proglottis, extending beyond longitudinal osmoregulatory canals ventrally, terminating anterior to cirrus sac and vagina. Gravid uterus sac-like, with anterior and posterior diverticula. Pyriform apparatus present. Parasites of Geomyidae (Rodentia).

Remarks. The genus *Pseudocittotaenia* has been retained for two species, *P. praecoquis* (Stiles, 1895) comb. nov. and *P. glandularis* sp. nov., both parasites of geomyid rodents in North America.

The genus is distinguished from all other related genera by the position of the uterus which is close to the anterior extremity of the proglottis, crosses the longitudinal canals ventrally rather than dorsally and in the tubular stage terminates anterior rather than posterior to the cirrus sac and vagina. This combination of characters does not occur in any of the related cestodes with paired genitalia, but it does occur in certain members of the genus *Paranoplocephala* Lühe, 1810 parasitising North American rodents, in particular *P. troeschi* Rausch, 1946. It is therefore reasonable to suggest that species of *Pseudocittotaenia* have arisen by duplication of the genitalia of North American species of *Paranoplocephala* and that their evolution has been parallel to the duplication of genitalia in European forms of *Paranoplocephala* which have given rise to the genus *Ctenotaenia* (see Spasskii, 1951, Tenora, 1976).

Pseudocittotaenia praecoquis (Stiles, 1895) comb. nov.
Figs 41-47, Table 10.

Ctenotaenia praecoquis Stiles, 1895 : 345 (as *praecoguus*).
Cittotaenia praecoquis (Stiles, 1895) Stiles and Hassall, 1896b : 407.
Neoctenotaenia praecoquis (Stiles, 1895) Tenora, 1976 : 13.
Cittotaenia megasacca Smith, 1951 : 313, figs 1-5.
Pseudocittotaenia megasacca (Smith, 1951) Tenora, 1976 : 15.

Types. From *Geomys bursarius* (Shaw, 1800), Ames, Iowa, USA, Osborne 1894, 2 specimens in USNM 11372.

Material Examined.

From *Geomys bursarius* (Shaw, 1800). Holotype and paratype.

Source : MNHN, Paris

From *Thomomys talpoides parowanensis* Goldman, 1938. 8 specimens, Griffith Creek, Tushar Mtns., Beaver County, Utah, USA, 12 August 1960, A. W. Grundmann, UU 14-20; 4 specimens, same locality, 10 August 1960, A. W. Grundmann, UU 14-21.

From *Thomomys talpoides clusius* Coves, 1875; 10 specimens, Savoy, Carbon County, Wyoming, USA, 1948, C. F. Smith; paratypes of *C. megasacca* in USNM and UNMC.

From *Thomomys talpoides tenellus* Goldman, 1939. 7 specimens, Moran, Wyoming, USA, 25, 26 June 1948, R. L. Rausch in colln. R. L. Rausch and UN.

Description. Short, broad worms with less than 100 proglottides in gravid strobilae. Scolex rounded anteriorly. Suckers oval, retracted within scolex. Neck absent. Proglottides craspedote, extended transversely. Mature proglottides with approximate length : width ratio of 1 : 12. Gravid proglottides with approximate ratio of 1 : 11. Terminal proglottides distinctly narrower than subterminal proglottides, with approximate ratio of 1 : 3. Muscular system not examined. Longitudinal osmoregulatory canals paired. Ventral canal wider than dorsal canal, situated medial to it. Transverse canal connects left and right ventral canals at posterior margin of each proglottis. Osmoregulatory canals of scolex not seen. Genital atrium deep, prominent, situated in middle of lateral proglottis margin in mature proglottides, near posterior extremity of lateral proglottis margin in gravid proglottides. Cirrus sac elongate, pyriform, thick-walled, extending just beyond ventral osmoregulatory canal. Cirrus elongate, coiled, uniformly covered with rows of short spines, surrounded by glandular cells. Ovoid internal seminal receptacle occupies one quarter to one third volume of cirrus sac. Ellipsoidal external seminal vesicle present, overlying proximal pole of cirrus sac. Vas deferens narrow, passes anteriorly and medially from seminal vesicle. Testes ovoid or spherical, numerous, arranged in 2-3 dorsoventral and 1-5 horizontal rows on dorsal aspect of medulla, in single band, entirely posterior to uterus. Few or no testes lateral to female genitalia. Considerable variation exists in number of testes lateral to female genitalia within individual strobilae. Testes occasionally extend as far laterally as longitudinal osmoregulatory canals and rarely lie lateral to canals. Vagina narrow, tube-like opens to genital atrium posterior to cirrus sac. Body of vagina lies ventral to cirrus sac on both sides of strobila. Vagina merges into enormous, pyriform seminal receptacle. Seminal receptacle persists in gravid proglottides. Ovary fan-shaped, composed of numerous clavate lobules, situated on ventral aspect of medulla. Vitellarium ovoid, posterior and dorsal to ovary. Mehlis' gland not seen. Single uterus per proglottis, developing as elongate, transverse tube close to anterior margin of proglottis. Uterus anterior to ovaries, seminal receptacles, crosses longitudinal osmoregulatory canals ventrally, terminating anterior to cirrus sac. Gravid uterus sac-like with numerous anterior and posterior diverticula. Anterior diverticula larger than posterior diverticula. Uterus eventually fills proglottis. Egg approximately spherical, thick-shelled. Oncosphere surrounded by pyriform apparatus which terminates in two elongate horns.

Remarks. The species was first described by Stiles (1895, 1896) under the names *Ctenotaenia praecoquis* and *Cittotaenia praecoquis* respectively, though the two specimens available to him were insufficient to allow a full description to be made. Subsequently, Smith (1951) redescribed *C. praecoquis* from *Thomomys talpoides* together with a new species which he named *Cittotaenia megasacca*. Unfortunately, he apparently did not examine the types of *C. praecoquis*, and it is evident from the re-examination of the types of both *C. praecoquis* and *C. megasacca*, made by the writer, that they are identical. Although the types of *C. praecoquis* are not well preserved, and the cirrus sac is smaller than in other specimens examined, the scolex, position of uterus and testis distribution are exactly as those seen also in the types of *C. megasacca*. Smith's (1951) specimens attributed to *C. praecoquis* are a distinct species, and are described below under the new name *Pseudocittotaenia glandularis*. Consequently, *C. megasacca* must fall as a synonym of *C. praecoquis*. However, the situation is complicated by the fact that recently (Tenora, 1976), these two have been placed in separate genera in two sub-families. *C. praecoquis* was transferred to a new genus *Neoctenotaenia* by Tenora (1976) having *Neo. ctenoides* as the type species. In the present revision, the genus *Neoctenotaenia* is placed as a synonym of *Mosgovoyia*. The genus *Pseudocittotaenia* was created by Tenora (1976) within the sub-

Source : MNHN, Paris

family *Monieziinae* Spasskii, 1951 for the species *P. megasacca* (Smith, 1951), *P. bequaerti* (Vigueras, 1943) and provisionally *P. rhea* (Fuhrmann, 1904), under the assumption that the uterus of each of these species was reticulate during the early part of its development. Smith's (1951) original description of *C. megasacca* indicated quite clearly that the uterus was initially tubular and that it subsequently developed anterior and posterior diverticula, an observation confirmed in the present redescription. Because of this, the genus must be transferred to the Anoplocephalinae. *P. bequaerti* and *P. rhea* are removed to the genus *Moniezia* Blanchard, 1891 (see below). Although *C. megasacca* falls as a synonym of *C. praecoquis*, the genus *Pseudocittotaenia* can be retained for *P. praecoquis*.

The above description differs from the original and that of Smith (1951) in a number of respects. However, since Stiles' material (1896) was poor, comparison with the original description will not be made in detail. Smith (1951) stated that the cirrus was unarmed, however, at least one of the paratypes of *C. megasacca* has several cirri everted and on them the armature is readily visible. It is not possible to see the cirrus armature on inverted cirri of the paratypes, however, it is readily seen on inverted cirri in other specimens examined. The description of the external seminal vesicle given by Smith (1951) implies that it is merely a passively produced dilation of the vas deferens when filled with sperm. Re-examination of his material indicates that the external seminal vesicle is invariably present and is easily distinguished before the male reproductive system has commenced functioning.

Although Smith (1951) in his drawings of the species shows testes anterior to the uterus, this situation was not found in re-examination. Occasional testes were found which overlapped the posterior margin of the uterus but none were found entirely anterior to it.

The occurrence of testes lateral to the female genitalia is highly variable and there may be no testes whatever lateral to the female genitalia (fig. 45). Although the testes extended to the longitudinal osmoregulatory canals quite frequently, only rarely did they lie lateral to the canals.

P. praecoquis is readily distinguished from the only other member of the genus *P. glandularis* by the lack of glandular cells around the distal extremity of the vagina, by the much longer, narrower cirrus sac, by the presence of an external seminal vesicle and by the occurrence of testes lateral to the female genitalia.

Stiles' (1896) and Smith's (1951) measurements of this species are included in Table 10. Smith's measurements were checked and since they appear to be accurate are not repeated. Only additional measurements made are tabulated.

TABLE 10. — MEASUREMENTS OF *PSEUDOCITTOTAENIA PRAECOQUIS* (in mm)

	Stiles (1896)	Smith (1951)		Present description
From	*Geomys bursarius*	From types of *C. megasacca*	From paratypes of *C. megasacca*	From *Thomomys talpoides* Utah and *Th. tenellus* Wyoming
Length	40	14-22		14-51
Width	5.5	4		5
No. proglottides	150	68-89		71-130
Scolex diam.	0.43 × 0.32	0. 65-0.82		0.50-0.65
Sucker size	0.16-0.128	0.22 × 0.19		0.16-0.22 × 0.17-0.20
Mature proglottides			1.6-2.2 × 0.15-0.20	1.3-2.8 × 0.2-0.4
Gravid proglottides			2.4-4.0 × 0.37-0.80	2.0-4.5 × 0.4-0.7
No. testes		100-135		80-110
Testis diam.		0.025-0.067		0.02-0.08

Source : MNHN, Paris

From	Stiles (1896)	Smith (1951)		Present description
	Geomys bursarius	From types of *C. megasacca*	From paratypes of *C. megasacca*	From *Thomomys talpoides* Utah and *Th. tenellus* Wyoming.
Cirrus sac	0.24 × 0.096	0.52 × 0.15		0.3-0.4 × 0.08-0.013
Internal semical vesicle			0.07-1.9 × 0.06-1.1	0.16-0.27 × 0.05-0.12
External seminal vesicle			0.2 × 0.07	0.12-0.20 × 0.05-0.1
Ovary			0.37-0.43 × 0.11-0.12	0.33-0.47 × 0.14-0.16
Vitellarium			0.06 × 0.04	0.04-0.05 × 0.08-0.10
Seminal receptacle	0.72-0.19	0.80 × 0.25		0.35-0.65 × 0.14-0.17
Dorsal osmoregulatory canal		0.019		0.02
Ventral osmoregulatory canal		0.32		0.07-0.1
Egg	0.032-0.036	0.038		0.04
Oncosphere		0.01		0.015
Pyriform apparatus			0.025	0.035

Pseudocittotaenia glandularis sp. nov.
Figs 48-54, Table 11.

Cittotaenia praecoquis (Stiles, 1895) Stiles and Hassall, 1896b *sensu* Smith, 1951 : 312-313.

Types. From *Thomomys talpoides clusius* Coves, 1875. Savoy, Carbon County, Wyoming, USA, 1948, C. F. Smith, holotype in USNM 4379.

Additional records. From *Thomomys talpoides wasatchensis* Durrant, 1946, Utah, USA (det. as *C. praecoquis*) (Frandsen and Grundmann, 1961).

Material examined.

From *Thomomys talpoides clusius* Coves, 1875. 1 specimen, Holotype, USNM.

From *Thomomys talpoides wasatchensis* Durrant, 1846. 4 slides of fragments, Monte Cristo Forest Camp, Cache County, Utah, USA, 10 July 1959, J. C. Frandsen and A. W. Grundmann, UU 41-3 ; 2 specimens, same locality, 11 July 1959, same collectors, UU 41-3.

Description. Scolex large, rounded, mildly four lobed. Proglottides craspedote, extended transversely. Mature proglottides with approximate length : width ratio of 1 : 7-1 : 12. Gravid proglottides, longer, relatively narrower, with ratio of 1 : 1.5-1 : 4. Muscular system not examined. Longitudinal osmoregulatory canals paired. Ventral canal wider than dorsal canal, situated medial to it. Transverse canal connects left and right ventral canals at posterior margin of each proglottis. Scolex osmoregulatory canals not seen. Genital atrium deep, narrow, situated in mid-region of lateral

Source : MNHN, Paris

proglottis margin. Cirrus sac ovoid or ellipsoidal, thick-walled, invariably extending just to aporal side of ventral osmoregulatory canal. Cirrus short, uncoiled, armature not seen. Cirrus surrounded by masses of intensely staining glandular cells. Ovoid internal seminal vesicle present, occupying up to one third to one half volume of cirrus sac. External seminal vesicle absent. Vas deferens narrow, slightly coiled, extending medially and anteriorly from cirrus sac. Testes ovoid or spherical, numerous, arranged in 2-3 dorso-ventral and 3-5 horizontal rows on dorsal aspect of medulla. Testes entirely posterior to uterus, invariably in single band, between female genitalia. Few testes lie dorsal to aporal part of ovary but none seen lateral to ovary. Vagina short, tube-like, opening to genital atrium posterior to cirrus sac. Distal extremity of vagina surrounded by mass of intensely-staining glandular cells. Vagina merges into enormous, pyriform seminal receptacle. Seminal receptacle persists in gravid proglottides. Ovary fan-shaped, composed of numerous clavate lobules situated on ventral aspect of medulla. Vitellarium roughly ovoid, lobulate, posterior and dorsal to ovary Mehlis' gland not seen. Uterus tubular, single, transverse, close to anterior proglottis margin. Uterus anterior to ovaries, seminal receptacles and testes, crossing longitudinal osmoregulatory canals ventrally, terminating close to dorsal canal, anterior to proximal pole of cirrus sac. Gravid uterus sac-like with anterior and posterior diverticula which may subdivide. Diverticula reduced or absent in region where uterus crosses osmoregulatory canals. Egg spherical thick shelled. Oncosphere surrounded by pyriform apparatus. Pyriform apparatus terminates in two elongate horns.

Remarks. This species was first described, but not illustrated, under the name *Cittotaenia praecoquis* by Smith (1951) and subsequently recorded from Utah by Frandsen and Grundmann (1961). Through the kindness of Dr. Grundmann, the latter specimens have been examined, and their co-identity with Smith's (1951) specimens established.

The species is here placed in the genus *Pseudocittotaenia* since it shares in common with the type species the situation of the uterus at the anterior extremity of the proglottis, passing the longitudinal canals ventrally and terminating at a level anterior to the cirrus sac. It is distinguished from *P. praecoquis* by the limitation of the testes to the area between the female genitalia and by masses of glandular cells surrounding the cirrus and the distal region of the vagina. The specific name is given on account of this latter characteristic.

Table 11. MEASUREMENTS OF *PSEUDOCITTOTAENIA GLANDULARIS* (in mm)

	Smith (1951)	Smith's material Holotype	Present description
	Thomomys talpoides Wyoming	*Thomomys talpoides* Wyoming Holotype	*Thomomys talpoides* Utah
Length	75-150		—
Width	2.0		2.5
Scolex diameter	0.74-0.85		0.65-0.66
Sucker diameter	0.26-0.29		0.25-0.30 × 0.20-0.30
Neck			0
No. proglottides	176-262		—
Mature proglottis		1.0-1.6 × 0.05-0.18	2.1-2.3 × 0.2-0.4
Gravid proglottis		1.6-2.0 × 0.8-0.85	1.2-2.2 × 0.35-1.0
Cirrus sac	0.24 × 0.09		0.15-0.24 × 0.06-0.09
Internal seminal vesicle		0.07 × 0.04	0.08-0.14 × 0.03-0.09

Source : MNHN, Paris

	Smith (1951)	Smith's material	Present description
	Thomomys talpoides Wyoming	*Thomomys talpoides* Wyoming	*Thomomys talpoides* Utah
No. testes	45-60		110
Testis size	0.039-0.054		0.04-0.06
Seminal receptacle		0.34-0.42 × 0.11-0.14	0.11-0.30 × 0.10-0.17
Ovary		0.32 × 0.17	0.27-0.40 × 0.20-0.25
Vitellarium		0.12 × 0.04	0.10-0.15 × 0.09-0.1
Dorsal osmoregulatory canal	0.015		0.01
Ventral osmoregulatory canal	0.05		0.04-0.12
Egg	0.035		0.04
Pyriform apparatus			—
Oncosphere	0.009		0.007

2. Subfamily MONIEZIINAE Spasskii, 1951

Genus *CITTOTAENIA* Riehm, 1881

Cittotaenia Riehm, 1881a : 200 ; Stiles and Hassall, 1896b : 407 ; Stiles, 1896 : 170 ; Douthitt, 1915 : 46-50 ; Baer, 1927 : 49-59 ; Fuhrmann, 1932 : 61 ; López-Neyra, 1947 : 227 ; Spasskii, 1951 : 413-420 ; Wardle and McLeod, 1952 : 365 ; López-Neyra, 1954 : 109-116 ; Yamaguti, 1959 : 200, 375-376 ; Tenora, 1976 : 14.

Types species. *Cittotaenia denticulata* (Rudolphi, 1804).

Diagnosis. Cestodes of moderate size. Strobila ribbon-like. Scolex small, unarmed. Suckers unarmed. Proglottides numerous (more than 100 in gravid strobilae), craspedote, extended transversely. Longitudinal osmoregulatory canals paired, with or without accessory longitudinal vessels and numerous anastomosing supplementary vessels connected to them. Transverse canal connects left and right ventral canals at posterior margin of each proglottis. Genitalia paired. Genital ducts pass longitudinal osmoregulatory canals dorsally. Cirrus sac dorsal to vagina on both sides of strobila. Internal and external seminal vesicles absent. Testes numerous, in single band or two groups. Seminal receptacle present. Ovaries situated in lateral quarters of proglottis medulla. Single transverse, tubular uterus, very slightly reticulated, not extending laterally beyond longitudinal osmoregulatory canals. Uterus develops anterior and posterior diverticula, finally becoming sac-like. Pyriform apparatus present. Parasites of Leporidae (Lagomorpha) and Chinchillidae (Rodentia).

Remarks. The definition of the genus given above is essentially similar to that of Spasskii (1951). It is left provisionally within the sub-family Moniezziinae, where it was placed by Spasskii, because the uterus is slightly reticulated. However, the extent of the reticulation is very slight in *C. denticulata* and usually consist of only 2 to 3 small loops in an otherwise simple tubular uterus,

Source : MNHN, Paris

differing considerably from the complex net-like uterus of the more typical members of the sub-family such as species of *Moniezia* and *Andrya*. In typical members of the subfamily Monieziinae, the net-like uterus gradually fills with eggs and loses its reticulated character whereas in *C. denticulata* the uterus develops anterior and posterior diverticula, a characteristic of the Anoplocephalinae. The situation is further complicated by the second species of the genus, *C. viscaciae* comb. nov. the morphology of which is still poorly known but which seems to have a slightly more reticulated uterus than *C. denticulata*. It is therefore proposed to leave the genus *Cittotaenia* within the subfamily Monieziinae pending further clarification of its taxonomic position.

The genus is differentiated from anoplocephaline genera parasitising rodents and lagomorphs by the slightly reticulated uterus, and within the Monieziinae, from *Diandrya* Darrah, 1930 by the slight reticulation of the uterus and the absence of a distinct prostate, and from the genus *Moniezia* again by the uterus, the lack of interproglottidal glands, the strong development of the cirrus sac and the relationships of vagina and cirrus sac on either side of the strobila.

Cittotaenia denticulata (Rudolphi, 1804)
Figs 55-65, Tables 12-13.

Taenia denticulata Rudolphi, 1804 : 81.
Alyselminthus denticulatus (Rudolphi, 1804) de Blainville, 1828 : 607.
Moniezia denticulata (Rudolphi, 1804) Blanchard, 1891 : 187.
Ctenotaenia denticulata (Rudolphi, 1804) Stiles and Hassall, 1896a : 6-9.
Cittotaenia denticulata (Rudolphi, 1804) Stiles and Hassall, 1896b : 407.
Taenia goezi Baird, 1853 : 78.
Moniezia goezi (Baird, 1853) Blanchard, 1891 : 444, 452-457, figs 21-25.
Ctenotaenia goezi (Baird, 1853) Railliet, 1893 : 278.
Cittotaenia latissima Riehm, 1881a : 200.
Dipylidium latissimum (Riehm, 1881) Riehm, 1881b : 583-590, pl. 5, figs 5, 15, 17, pl. 6, fig. 2.
Taenia latissima (Riehm, 1881) Neumann, 1888 : 426.

TYPES. In Berlin Museum (not examined).

MATERIAL EXAMINED.

From *Oryctolagus cuniculus* Linnaeus, 1758. 1 specimen, no locality or date, BM 1957.5.1.9-10; 8 specimens, Milford, Surrey, England, 8 August 1974, A. Mead-Briggs, UMVS; 2 specimens, Camargue, France, January 1935, C. Joyeux, UN; 1 specimen, Si Allal Tazi, Morocco, 15 April 1942, C. Joyeux, UN; 1 specimen, Paris, France, 1930, C. Joyeux, UN.

DESCRIPTION. Large, broad, ribbon-like worms. Scolex small, quadrate, distinctly separated from strobila, four lobed with sucker on each lobe. Neck absent. Proglottides extended transversely, craspedote with narrow, slightly undulating velum overhanging adjacent proglottis. Mature proglottides with approximate length : width ratio of 1 : 8-1 : 10. Gravid proglottides with ratio of 1 : 3-1 : 8. Longitudinal musculature moderately developed, arranged in two irregular rows of oval or elongate bundles in cortex. Bundles of two rows of approximately equal size. Transverse muscles filiform, in band internal to longitudinal muscles. Dorso-ventral muscles fine, crossing medulla and cortex at irregular intervals. Longitudinal osmoregulatory canals variable in number. Dorsal canal narrow, thick-walled, surrounded externally by layer of muscle cells. Usually 2-4 major ventral canals situated both lateral and medial to dorsal canal. 1-2 additional smaller canals may be present. Transverse canal connects ventral canals at posterior margin of each proglottis. Irregular anastomoses connect various central canals as well as anastomosing network of canals connecting transverse canals

Source : MNHN, Paris

of adjacent proglottides. In scolex, canals consist of paired dorsal and paired ventral canals only. Posterior to suckers, canals of each side describe prominent lateral loop, return to near midline and extend anteriorly between suckers. Transverse anastomosis connects ventral canals from each side. Similar anastomosis connects two dorsal canals. Four canals extend anteriorly from level of two transverse anastomoses. Two short dorso-ventral loops connect dorsal and ventral canal on each side of scolex. Genital atrium deep, narrow, situated in posterior half of lateral proglottis margin dividing margin in ratio of 2 : 1. Genital papilla present in fully mature proglottides as prominent dome-shaped projection close to postero-lateral corner of proglottis. Cirrus sac large, oblong, thick-walled, surrounded by layer of polygonal parenchymatous cells. Cirrus short uncoiled. Distal region of wider diameter, heavily armed with rows of spines. Proximal region unarmed, slightly dilated when filled with sperm. Internal and external seminal vesicles absent. Vas deferens narrow, thin-walled, coiled, surrounded by layer of glandular cells. Vasa efferentia not seen. Testes numerous in 2-3 transverse and 6-8 horizontal layers on dorsal aspect of medulla. Testes usually lie both anterior and posterior to uterus, but in some immature proglottides may lie entirely posterior to uterus. Testes lie between female genitalia, overlapping ovary and vitellarium dorsally, but never extending laterally beyond them. Vagina narrow, uncoiled, opens to genital atrium posterior to cirrus sac. Vagina lies ventral to cirrus sac on both sides of strobila. Seminal receptacle oval or circular in dorso-ventral view, dorsal to ovary. Ovary circular with central reservoir and numerous elongate clavate lobules radiating anteriorly, posteriorly laterally, medially and dorsally. Vitellarium reniform to U-shaped, lobulate, posterior and dorsal to centre of ovary. Mehlis' gland spherical, lying between arms of vitellarium, slightly dorsal to them. Uterus single in each proglottis, transverse, tube-like with small number of reticulations and vestigial anterior and posterior diverticula. Developing uterus slightly reticulate with 1-4 loops in each uterus, or rarely non-reticulate in the form of a simple transverse tube. Numerous anterior and posterior diverticula present. Uterus does not cross longitudinal osmoregulatory canals. Gravid uterus sac-like, filling proglottis medulla. Reticulations not visible. Egg spherical, thick-shelled. Oncosphere surrounded by pyriform apparatus drawn out into two elongate horns. Horns rarely subdivided giving appearance of three-horned pyriform apparatus.

Remarks. This species has been well described in the past (John, 1926) and is sufficiently characteristic morphologically that confusion with other species is not likely to occur. The present description differs little from that of John (1926). The number of ventral osmoregulatory canals was found to be more variable and a network of accessory canals connecting transverse canals of adjacent proglottides, similar to that in *Mosgovoyia pectinata* was found. John (1926) presumably saw these accessory canals but simply stated that "secondary longitudinal canals occur". He also stated that whilst secondary canals were present in mature proglottides, only two ventral canals were present in younger proglottides. In the material studied here, accessory canals were seen within 2 mm of the scolex and even proglottides with only genital anlagen in them were found with a complex network of accessory canals.

Riehm (1881a) described the pyriform apparatus as terminating in elongate filaments. Although not found in the present study, it may be that the material available was not fully developed. One embryo was found with a three-horned pyriform apparatus.

The relationships of uterine development to the systematic position of the parasite have been discussed earlier.

Edelényi (1965) identified *C. denticulata* from *Lepus europaeus* in Hungary, but from the figure provided, the parasite in question appears to be *M. pectinata*. In a subsequent paper (Edelényi, 1966), *C. denticulata* is again reported from *L. europaeus* in Hungary, but as there is no description or diagram from which to check the identification, the record has been included in Table 13, but with reservation.

Joyeux and Gaud (1945) reported *M. pectinata* from *Oryctolagus cuniculus* in Morocco, but re-examination of their material has revealed that it is in fact *C. denticulata*.

Source : MNHN, Paris

TABLE 12. — MEASUREMENTS OF *CITTOTAENIA DENTICULATA* (in mm)

	Stiles (1896)	John (1926)	Baer (1927)	Arnold (1938)	Present description
Length	400-500	30-70	400-500	260	—
Width	15	11-13	15	8.5	11
Scolex diam.	0.8 × 0.63	0.75-1.18 × 0.43-0.52	0.8-1.0	0.10-0.76	0.75-0.90
Sucker diam.		0.23-0.29	0.2-0.3	0.23-0.30	0.24-0.26 × 0.21-0.24
Neck	0			0.21-0.92	0
No. proglottides	200	300		260	—
Mature proglottides					5.7 × 0.6-0.7
Gravid proglottides					4-11 × 1.7-3.0
Cirrus sac	1.12 × 0.32	0.75 × 0.26	1.12 × 0.3	0.50-0.97	0.6-0.95 × 0.23-0.25
No. testes			100	225-250	200
Testis size	0.115	0.129	0.100	0.041-0.12	0.04-0.12
Seminal receptacle		0.2-0.4 × 0.15-0.2			0.36-0.45 × 0.31-0.35
Ovary		1.4		0.32-1.42	0.1-1.0 × 0.4-0.8
Vitellarium		0.5			0.28-0.75 × 0.15-0.28
Mehlis' gland					0.12
Dorsal osmoregulatory canal					0.02-0.06
Ventral osmoregulatory canals					0.06-0.18
Egg	0.052-0.060	0.054	0.052-0.060	0.046-0.075	0.065
Pyriform apparatus					0.038
Oncosphere		0.008			0.015

TABLE 13. — HOST RECORDS OF *CITTOTAENIA DENTICULATA*

Host	Locality	Reference
Oryctolagus cuniculus Linnaeus, 1785		
	Great Britain	Mead-Briggs and Page (1975)
	Surrey, England	Mead-Briggs and Vaughan (1973)
	Northumberland, England	Boag (1972)
	England, Wales	Baylis (1939)
	Aberystwyth, Wales	John (1926), Evans (1940)
	Wales	Stephens (1952)
	Scotland	Fahmy (1960)
	Granada, Madrid, Spain	López-Neyra (1947, 1954)
	France	Du Buysson (1904)
	France, Germany	Stiles (1896)

Source : MNHN, Paris

Host	Locality	Reference
	Hamburg, Germany	Arnold (1938)
	Alsace, France	Galli-Valerio (1930a)
	Richelieu, France	Dollfus (1961)
	Ile de St. Pierre, Switzerland	Galli-Valerio (1910, 1930a)
	Morocco (det. as *M. pectinata*)	Joyeux and Gaud (1945)
Lepus europaeus Pallas, 1778		
	Scotland	Cameron and Parnell (1933)
	? Hungary	Edelényi (1966)
Lepus timidus Linnaeus, 1758		
	Scotland	Cameron and Parnell (1933)
	Sweden	Burgaz (1970)

Cittotaenia viscaciae (Spasskii, 1951) comb. nov.
Figs 66-72, Table 14.

Mosgovoyia viscaciae Spasskii, 1951 : 296-297.
Cittotaenia pectinata (Goeze, 1782) *pro parte* Joyeux and Dollfus, 1931 : 155.

Types. Single specimen from *? Lagostomus maximus* (Desmarest, 1817) (syn. *Viscaeia viscacia* (Molina, 1782)), Valdivia, Chile. Whole mount and serial sections in UN.

Material examined. Type.

Description. Moderate sized worm. Scolex small, rounded anteriorly. Suckers cup-shaped, opening circular. Scolex merges imperceptibly into unsegmented neck region. Proglottides extended transversely, craspedote with broad, straight-edged velum overbanging adjacent proglottis. Mature proglottides with approximate length : width ratio of 1 : 5. Gravid proglottides with ratio of 1 : 4.5. Longitudinal musculature weakly developed, arranged in two rows of small, oval bundles containing 3-15 fibres per bundle, in ring around inner edge of cortex. Transverse muscles fine, in band internal to longitudinal muscles. Dorso-ventral muscles fine, few in number, irregularly arranged. Longitudinal osmoregulatory canals paired. Ventral canal wider than dorsal. Transverse canal connects left and right ventral canals at posterior margin of each proglottis. Small accessory longitudinal canals associated with transverse canal. Broad genital papilla present in many proglottides, in posterior half of lateral proglottis margin. Genital atrium shallow. Cirrus sac large, oblong. Walls of cirrus sac thick, muscular in mid and proximal regions, diminishing in thickness distally. Cirrus uncoiled, armed with numerous, awl-like, spirally-arranged spines. Mid region of cirrus unarmed. Spines were absent from everted cirri, presumably due to tardy fixation of specimen. Proximal region of cirrus slightly dilated with sperm. Internal and external seminal vesicles absent. Vas deferens thin-walled, slightly coiled, passing medially in arc, dorsal to ovary, adjacent to seminal receptacle. Vasa efferentia not seen. Testes numerous, situated in two entirely separate groups in posterior part of proglottis, on dorsal aspect of medulla in 2-5 horizontal and 1-4 transverse rows. Testes extend lateral to female genitalia, overlying vitellarium dorsally. Vagina opens to genital atrium posterior to cirrus sac via narrow invaginated extension of atrium. Vagina narrow, thin-walled, posterior and ventral to cirrus sac. Seminal receptacle small, clavate, dorsal to centre of ovary. Ovary circular in dorso-ventral view, situated on ventral aspect of medulla, with central reservoir and numerous

Source : MNHN, Paris

clavate lobules radiating from it. Vitellarium U-shaped, lobulate, dorsal to ovary. Anterior parts of vitellarium lie either side of seminal receptacle. Mehlis' gland not seen. Testes, vitellaria and seminal receptacles persist after involution of ovary. Uterus slightly reticulated in early stage of development, lying on ventral aspect of medulla. Ring of uterus surrounds each seminal receptacle with major branch anterior and one posterior to testes. Gravid uterus sac-like, non-reticulated, filling proglottis. Egg spherical, thick-shelled. Oncosphere surrounded by pyriform apparatus drawn into two elongate horns.

REMARKS. This specimen was briefly described by Joyeux and Dollfus (1931) amongst a collection of cestodes sent to them from the Münich Museum. Its morphological features differed somewhat from those of *M. pectinata*, particularly with respect to the occurrence of testes in two groups, a feature which these authors noted was characteristic of *M. ctenoides* rather than *M. pectinata*. However they cited Baer's revision of the Anoplocephalidae as evidence that *M. pectinata* was a highly variable species and placed their specimen under this name. Spasskii (1951) subsequently erected a new species, *Mosgovoyia viscaciae* for the specimen in spite of the fact that he had only Joyeux and Dollfus' (1931) quite inadequate description from which to judge its taxonomic position.

Although only the one type specimen was available for description, and the state of the specimen is now such that a full description cannot be made, the features of the worm described above indicate quite clearly that it does not belong to the genus *Mosgovoyia* but that it probably belongs to the genus *Cittotaenia*. The cestode is similar to *C. denticulata* in many respects, particularly in possessing a slightly reticulated uterus, a large, oblong, cirrus sac and heavily-armed cirrus as well as in the structure of the ovary which in both species is circular with lobules radiating from a central reservoir, rather than being fan-shaped as is the case with all other species dealt with herein. *C. viscaciae* can be distinguished from *C. denticulata* by the occurrence of testes in two groups in the posterior part of the proglottis and by the lack or at least the small number of accessory osmoregulatory canals.

The host of this species cannot be stated with certainty. Joyeux and Dollfus (1931) gave as the host " *Viscacia viscacia* (Molina) syn. *Lagostomus trichodactylus* Brookes " apparently deriving the host nomenclature from Trouessart (1899). The current name of *L. trichodactylus* is *Lagostomus maximus* (Desmarest, 1817) (see Cabrera 1961) however, it does not occur in Chile which was the collection locality given by Joyeux and Dollfus (1931). Both Osgood (1943) (p. 137) and Cabrera (1961), however, give *Lepus viscacia* Molina, 1782 as a synonym of *Lagidium viscacia* (Molina, 1782), the common mountain viscacia of Chile, which occurs, according to Osgood (1943) in the provinces of Aconcagua, Santiago and Valparaiso, which are not too distant from Valdivia. It is also possible that the initial identification of the host was merely the vernacular name " viscacia " which was taken to be the " Argentinian or plans viscacia ", *L. maximus* rather than a " mountain viscacia " belonging to the genus *Lagidium* Meyen, which occur in Peru and Chile. Since there are several species in the genus *Lagidium*, it is not possible to suggest which one is the most likely host. The true host of *C. viscaciae* is of some importance since another anoplocephalid, *Cittotaenia quadrata* von Linstow, 1904 has been described from *Lagidium peruanum* Meyen, 1833, in Peru. The descriptions and extant material of *C. quadrata* are so poor as to make the determination of its taxonomic position impossible, however, in the slides that do exist it appears to have a cirrus sac similar to *C. viscaciae*. It is therefore not impossible that *C. viscaciae* might be a synonym of *C. quadrata* though without new collections of cestodes from *Lagidium peruanum* the matter cannot he pursued further.

Source : MNHN, Paris

TABLE 14. — MEASUREMENTS OF *CITTOTAENIA VISCACIAE* (in mm)

	Joyeux and Dollfus (1934)	Present description
Length		106
Width		6
Scolex diameter	0.50	0.45
Sucker diameter		0.15-0.16
No. proglottides		157
Mature proglottis		5.5 × 1.0
Gravid proglottis		5.5 × 1.5
Cirrus sac	0.72 × 0.15	0.55-0.80 × 0.22-0.25
Internal seminal vesicle		—
No. testes	140-160	120
Size testes	0.06	0.06
Seminal receptacle		0.22 × 0.17
Ovary	0.6	0.5 × 0.5
Vitellarium	0.225	0.30 × 0.26
Egg	0.06	0.075
Pyriform appparatus		0.020
Oncosphere		0.010

3. — Species Referred to other genera of Anoplocephalidae

Subfamily ANOPLOCEPHALINAE

Genus *STRINGOPOTAENIA* gen. nov.

TYPE SPECIES. *Stringopotaenia psittacea* (Fuhrmann, 1904).

DIAGNOSIS. Anoplocephaline cestodes with paired reproductive organs. Scolex unarmed. Suckers unarmed. Proglottides numerous (greater than 100 in gravid strobila), craspedote, extended transversely. Longitudinal osmoregulatory canals paired. Transverse canal connects left and right ventral canals at posterior margin of each proglottis. Genital ducts cross longitudinal osmoregulatory canals dorsally. Cirrus sac dorsal to vagina on right hand side of strobila, ventral to it on left hand side. Internal seminal vesicle present, external vesicle absent. Testes numerous, scattered throughout medulla. Seminal receptacle present. Ovaries situated in lateral quarters of proglottis, uterus in middle of proglottis with two U-shaped loops passing anteriorly over vitellaria. Gravid uterus of similar shape with anterior and posterior diverticula. Egg with pyriform apparatus. Parasites of Psittacidae (Aves).

REMARKS. See below.

Source : MNHN, Paris

Stringopotaenia psittacea (Fuhrmann, 1904) comb. nov.
Figs 73-78, Table 15.

Cittotaenia psittacea Fuhrmann, 1904 : 358-386.
Paramonieia psittacea (Fuhrmann, 1904) Spasskii, 1951 : 303-305, fig. 143.

Types. Single specimen, from *Stringops habroptilus* Gray, 1845 (Psittacidae : Stringopinae), New Zealand, as 19 slides of histological sections, UN.

Material examined. Type.

Description. Scolex at anterior extremities of suckers square in transverse section. Sections posterior to suckers cross-shaped, indicating four lobes to scolex. Proglottides craspedote with narrow, straigbt-edged velum, extended transversely. Mature proglottides with approximate length : width ratio of 1 : 9. Gravid proglottides with ratio of 1 : 6. Longitudinal musculature strongly developed, arranged in bundles of variable size around inner margin of cortex. Two to three layers of bundles present. Transverse muscles fine, forming band internal to longitudinal muscles. Dorso-ventral muscles not seen. Longitudinal osmoregulatory canals paired. Ventral canal wider than dorsal canal. Transverse canal connects left and right ventral canals at posterior margin of each proglottis. Longitudinal nerve lateral to canals. Genital atrium insignificant, in posterior half of lateral proglottis margin. Cirrus sac oblong, elongate, extending beyond osmoregulatory canals. Cirrus coiled, thick-walled, muscular, armed witb sbort stout bristles. Internal seminal vesicle elongate. External seminal vesicle absent. Vas deferens prominent, greatly coiled, surrounded by pale-staining, polygonal cells. Coils of vas deferens extend in transverse plane across entire width of medulla anterior to cirrus sac, and in borizontal plane from lateral edge of ventral osmoregulatory canal to ovary. Proximal coils of vas deferens smaller in diameter, without surrounding polygonal cells. Vas deferens runs to dorsal aspect of medulla, divides into numerous vasa efferentia. Testes numerous, in 2-3 transverse layers and 6-8 horizontal layers on dorsal aspect of medulla. Testes extend throughout medulla and are limited laterally by osmoregulatory canals. Testes lie anterior and posterior to the uterus extend lateral to female genitalia and overlie ovary, cirrus sac and vas deferens dorsally. Vagina opens to genital atrium posterior to cirrus sac. Vagina lies ventral to cirrus sac on right hand side of strobila and dorsal to it on left hand side. Distal vagina tube-like, narrow, lined internally witb hairs, vaginal wall tbick, muscular, surrounded by layers of glandular cells. Proximal vagina (medial to osmoregulatory canals) tbin-walled, ending in elongate, pyriform, thin-walled sac without hairy lining or glandular cells. Seminal receptacle circular in dorso-ventral view, dorsal to ovary. Ovary in lateral part of proglottis medulla fan-shaped, composed of numerous clavate lobules, situated on ventral aspect of medulla. Vitellarium oblong or reniform, dorsal and posterior tc ovary. Mehlis' gland spherical, anterior and dorsal to vitellarium. Oocapt present at origin of oviduct. Oviduct joins duct from seminal receptacle forming short fertilisation duct which joins with vitelline duct and common duct formed passes anteriorly to Mehlis' gland, emerges on dorsal side of gland and continues anteriorly and ventrally to uterus. Uterus single, transverse, tube-like, situated in posterior half of proglottis close to transverse osmoregulatory canal. Uterus bends anteriorly forming loop over vitellarium, dorsal to ovary, ventral to seminal receptacle and Mehlis' gland. Junctions of transverse body of uterus with loops marked by short, posteriorly-directed diverticula. In gravid proglottides, uterus crosses longitudinal canals dorsally, extends to postero-lateral corners of proglottis. Gravid uterus sac-like, with anterior and posterior diverticula but retaining anterior loops over sites of vitellaria. Egg approximately spherical, thick shelled. Inner membrane present. Oncosphere surrounded by pyriform apparatus terminating in two elongate borns. One or two sets of rudimentary genitalia present near centre of each proglottis. If one set present, situated

Source : MNHN, Paris

to one side of mid-line. Uterine duct usually present, with ovarian lobules and/or vitellarium. Mehlis' gland occasionally present. Coiled portion of vas deferens present in one proglottis.

Remarks. Although repeating in many instances the observations made by Fuhrmann (1904, 1908, 1921) on this species, the additional features described significantly alter the taxonomic position of the parasite. Minor differences exist between the present observations and those of Fuhrmann. Fuhrmann (1921) gave as the testis diameter 0.08-0.16 mm compared with the present finding of 0.065 mm, a difference for which there is no obvious explanation. He also stated that testes lie entirely anterior to the uterus, yet a small number can be found overlapping the uterus dorsally with others entirely posterior to it.

The major morphological feature upon which the taxonomic position of the parasite appears to hinge and which Fuhrmann did not describe in detail is the structure of the uterus. The double U-shape of the uterus in both mature and gravid proglottides indicates a much closer affinity with the genus *Paronia* Diamare, 1900 than with *Cittotaenia*, *Ctenotaenia* or *Paramoniezia* into all of which genera the parasite has formerly been placed. In the genus *Paronia*, the mature proglottis possesses two uteri each in the form of an inverted U over the female genital complex. In the gravid proglottis, the uteri may fuse to give a double U-shaped structure. A similarly-shaped uterus is present in *Stringopotaenia psittacea*. The morphology of the uterus was not easy to study as only serial sections were available. Most were oblique and showed only one of the U-shaped components, however, a few sections were found which indicated the shape of the entire uterus and one of these has been drawn (Fig. 74). The few sections that show the entire length of the uterus are not the most convincing for demonstrating the U bend over the female genitalia, so a drawing is also included (Fig. 76), showing half the uterus with a prominent bend over the remnants of the vitellarium. The same general uterine shape is also evident in mature proglottides, the U loop over the vitellarium being demarcated on either side by two short, posteriorly-directed diverticula. *S. psittacea* differs from typical representatives of the genus *Paronia* in having a single uterus per proglottis instead of two uteri which may fuse, in the relative positions of cirrus sac and vagina on either side of the strobila and in the accessory female genital organs present in the centre of the proglottis. Since *S. psittacea* cannot readily be accommodated in the genus *Paronia*, a new genus has been proposed, the name being derived from that of the host.

Spasskii (1951) used the position of the vagina dorsal to the cirrus sac on one side of the strobila and ventral on the other side to place *S. psittacea* in the genus *Paramoniezia* Maplestone and Southwell, 1923, apparently overlooking the fact that the type species of the genus, *P. suis* Maplestone and Southwell, 1923 was described as having the vagina on one side of the cirrus sac on the right hand side of the strobila and either dorsal or ventral on the other side of the strobila. The situation of the genital ducts in *S. psittacea* is in fact the same as in the genus *Moniezia*. In addition, Beveridge (1976) re-examined the type of *P. suis* and found that Maplestone and Southwell (1923) had erred in their description of the relationships of cirrus sac and vagina in this species and that the cirrus sac lay on the same side of the vagina on both sides of the strobila. Although Beveridge (1976) retained and redefined the genus *Paramoniezia*, the present redescription indicates clearly that *S. psittacea* does not belong within it.

Baer (1927) placed *Paramoniezia suis* as a synonym of *S. psittacea* (then *Cittotaenia psittacea*), saying that he could find no differences between them. This statement must be due in part to the extremely poor state of the type and only specimen of *P. suis*. So poor are the slides that an adequate redescription cannot be given, however, the two species differ markedly in the morphology of the seminal receptacle as well as in the vas deferens which in *S. psittacea* is an enormous coiled structure surrounded by prostatic cells and in *P. suis* a simple coiled tube.

The Australian representatives of the genus *Paramoniezia* were discussed by Beveridge (1976). Two valid species were admitted, the type species, *P. suis* and a new species *P. johnstoni* Beveridge, 1976. The only other species in the genus, *P. phacochoeri* was considered a *species inquirenda*. The removal of *P. psittacea* to a new genus leaves in the present revision the genus *Paramoniezia* as a wholly Australian one with only two species.

Source : MNHN, Paris

Apart from morphological similarities, the genera *Paronia* and *Stringopotaenia* are both found in Psittacidae. All of the other anoplocephalid genera found in Psittacidae have single genitalia. *Aporina* Fuhrmann, 1902, *Bioporuterina* Burt, 1973, *Hemiparonia* Baer, 1927, *Paronia* Diamare, 1900 and *Triuterina* Fuhrmann, 1921 are distributed through Africa, America, Asia and Australia whilst *Pulluterina* Smithers, 1954 is known only from New Zealand. When compared with *Pulluterina nestoris* Smithers, 1954, the resemblance between the mature proglottis and half of that of *S. psittacea* is striking. The morphology of the uterus in mature proglottides is very similar, although the gravid uterus in *P. nestoris* has elongate anterior and posterior diverticula unlike *S. psittacea*. Several instances are known in which two genera differ only in possessing single or paired genitalia and it is supposed that the former arose from the latter (Baer, 1955). *Pulluterina* and *Stringopotaenia* may be related in the same way and hence similarities between *Paronia* and *Stringopotaenia* may be due to convergence. It is possible to interpret the extra sets of female genitalia which occur so regularly in the centre of the proglottides of *S. psittacea* as a legacy of the duplication of genitalia. Similar vestigial genitalia occur less frequently in species of *Ctenotaenia* and *Mosgovoyia*.

New Zealand has two genera of indigenous and quite unique parrots, the keas, *Nestor* spp. (subfamily Nestorinae) which constitutes the only genus in the subfamily, parasitised by *Pulluterina nestoris* (see Smither, 1954) and the kakapo, *Stringops habroptilus* (subfamily Stringopinae) again the only genus in the subfamily, parasitised by *S. psittacea*. The long separation of New Zealand from other continents and its unique parrot fauna parallel the differences in the two endemic genera of parrot cestodes when compared with the anoplocephalid genera of Psittacidae elsewhere in the world.

It is to be regretted that the description of *S. psittacea* must be based on a single specimen, however, the host is now almost extinct (Merton, 1975) and the likelihood of obtaining additional material is small.

TABLE 15. — MEASUREMENTS OF *STRINGOPOTAENIA PSITTACEA* (in mm)

	Fuhrmann (1904)	Fuhrmann (1921)	Present description
Length	100	130	—
Width	6.0	6.5	—
Scolex diameter	0.23	0.57	0.55
Sucker diameter		0.23 × 0.26	0.18-0.19
Mature proglottis			3.9 × 0.4
Gravid proglottis			4.0 × 0.75
Cirrus sac	0.52 × 0.02	0.5 × 0.05	0.58 × 0.10
Internal seminal vesicle		—	—
No. testes		approx. 200	approx. 200
Testis size		0.08-0.16	0.065
Seminal receptacle			—
Ovary		0.8 × 0.28	0.63 × 0.26
Vitellarium		0.28	0.23 × 0.13
Mehlis' gland			0.08
Dorsal osmoregulatory canal			0.013-0.040
Ventral osmoregulatory canal			0.16-0.23
Egg			0.06
Pyriform apparatus		0.021	—
Oncosphere			0.015

Source : MNHN, Paris

Subfamily MONIEZIINAE

Moniezia rhea (Fuhrmann, 1904) comb. nov.
Figs 79-90, Table 16.

Cittotaenia rhea Fuhrmann, 1904 : 386-387.
Ctenotaenia rhea (Fuhrmann, 1904), Spasskii, 1951 : 272-273, fig. 128.
Pseudocittotaenia rhea (Fuhrmann, 1904) Tenora, 1976 : 15.

Types. From *Rhea americana* Linnaeus, 1758, no collection data, alcohol specimens, whole mounts and serial sections, in UN.

Material examined. Types. 4 specimens from *Rhea americana*, Brazil, in HCIOC and UN.

Description. Small, narrow worm. Scolex very large, quadrate, forming four bulbous lobes with very large, oval, muscular suckers. Neck long, narrow in relaxed specimens, absent in contracted specimens. Proglottides craspedote with narrow, straight-edged velum overhanging adjacent proglottis, extended transversely. Mature proglottides with approximate length : width ratio of 1 : 5-1 : 9. Gravid proglottides with ratio of 1 : 7-1 : 9. Cortex extremely thick, approximately 5 times as wide as medulla. Longitudinal musculature very powerfully developed. Inner longitudinal muscle fills two-thirds thickness of cortex, arranged in bundles of variable size with 2-40 fibres per bundle. Bundles arranged in 6-8 irregular layers around inner part of cortex. Outer longitudinal muscles arranged in ring of small bundles, 2-3 deep, with 2-10 fibres per bundle. Two rings of longitudinal muscle separated by narrow band of parenchyma. Transverse muscles fine, arranged in narrow band internal to longitudinal muscles. Dorso-ventral muscles well developed, single, irregularly arranged, crossing medulla at irregular intervals, passing between bundles of inner longitudinal muscles. Longitudinal osmoregulatory canals paired. Ventral canal straight-sided, of considerable internal diameter. Transverse canal connects left and right ventral canals at posterior margin of each proglottis. Dorsal canal much narrower than ventral canal, present in scolex and neck only. Absent in strobila posterior to level of proglottides with genital analgen. Genitalia paired. Genital ducts cross longitudinal osmoregulatory canals dorsally. Genital atrium very small, situated in posterior half of lateral proglottis margin. Cirrus sac elongate, extremely narrow, extending beyond osmoregulatory canal. Cirrus very slightly coiled, narrow, heavily armed with short stout bristles. Armature seen only in sections of cirri in gravid proglottides. Internal and external seminal vesicles absent. Vas deferens thin-walled, greatly coiled. Coils extend in transverse plane from medial border of ventral osmoregulatory canal to poral border of vitellarium, dorsal to ovary. In longitudinal plane, coils extend from transverse osmoregulatory canal at anterior margin of proglottis to vitellarium. Following reduction in diameter, vas deferens runs along dorsal edge of medulla with vasa efferentia branching from it. Testes numerous, occupying whole dorsal plane of medulla in single transverse layer and 3-5 longitudinal rows. Testes fill entire space between transverse osmoregulatory canals and extend laterally beyond female genitalia to ventral osmoregulatory canals. Vagina very narrow, surrounded by loose layer of cells. Opens independently to genital atrium posterior to cirrus sac. Cirrus sac dorsal to vagina on right hand side of strobila, ventral to it on left hand side. On left hand side, vagina crosses cirrus sac medial to ventral osmoregulatory canal and passes to ventral side of medulla. Vagina terminates in elongate, thin-walled seminal receptacle, immediately dorsal to ovary. Seminal receptacle sinuous, widest at poral end, diminishing in size aporally. Ovary fan-shaped, composed of numerous clavate lobules, close to ventral osmoregulatory canal on ventral aspect of medulla. Vitellarium ovoid, lobulate, posterior and dorsal to ovary. Hemispherical reservoir present on dorsal surface

Source : MNHN, Paris

at apex of ovary. Ovarian duct curves dorsally joining with aporal end of seminal receptacle to form short, dorsally-directed fertilisation duct. Vitelline duct joins fertilisation duct and common duct coils medially and dorsally, passes along dorsal margin of medulla then anteriorly and ventrally to uterus. Mehlis' gland greatly reduced. Represented only by layer of spindle-shaped cells surrounding uterine duct as it passes along dorsal border of medulla. Uterus net-like, restricted to medulla in early stages of development. During filling, uterus becomes complex tubular network extending across ventral aspect of medulla, crossing ventral osmoregulatory canal dorsally. Gravid uterus sac-like, extending to lateral margins of proglottis, with only vestiges of initial diverticula remaining. Egg spherical, thick-shelled. Inner membrane present. Pyriform apparatus with two short polar horns in early stage of development. Fully developed pyriform apparatus with two narrow, apposed horns ending in small hollow cone.

REMARKS. Only a limited amount of material of this species was available for study. The type material was found to be in a very poor state of preservation as whole specimens stained very poorly and histological sections showed the internal organs in an advanced state of autolysis. Fortunately, four further specimens from *Rhea americana* from Brazil were obtained. Although contracted and impossible to study as whole mounts, serial sections showed the specimens to be in an excellent state of preservation and it was possible to establish the morphology of the species from them.

Fuhrmann's descriptions (1904, 1021) were necessarily incomplete as they were based on rather unsatisfactory specimens, however some additional morphological details were obtained from the types. Fuhrmann (1921) described and illustrated a poorly developed pyriform apparatus with two short polar horns, as shown in fig. 80. Spasskii (1951) speculated that this was merely a stage in the development of the pyriform apparatus as identical forms occurred in the development of the structure in *Moniezia* spp. His speculations are correct as in other parts of the type material there are fully developed eggs in which the pyriform apparatus is drawn into two parallel, elongate horns terminating in a small conical " cap ", identical to that of *Moniezia expansa* (Rudolphi, 1810).

In spite of a relatively full account of the morphology of the parasite, its taxonomic position is not easy to establish. Using Spasskii's keys (1951), it belongs to the genus *Moniezia* Blanchard, 1891 and does in fact have numerous features in common with this genus, namely that the uterus is highly reticulated, internal, and external seminal vesicles are absent, the vagina lays dorsal to the cirrus sac on one side of the strobila and ventral to it on the other and in the structure of the pyriform apparatus. A number of differences exist however. The scolex and suckers are extraordinarily strongly developed as is the longitudinal musculature, the cirrus sac is extremely long and slender, the vas deferens is a very large, greatly coiled organ, the seminal receptacle is sinuous but has its greatest internal diameter at its poral extremity (this is similar to *Moniezia mettami* Baylis, 1934 redescribed by Mahon, 1954), and Mehlis' gland which is a prominent spherical organ in species of *Moniezia* is reduced to a single layer of cells. Yet none of these criteria in themselves appear to be sufficient for the erection of a new genus. Furthermore, as is evident from this revision, the Monieziinae in Central and South American animals appear to be in need of revision from further collections. Apart from *Moniezia rugosa* (Diesing, 1850) in South American primates, the present revision has added *M. bequaerti* (Vigueras, 1943) comb. nov. from a Central American rodent to the genus. In addition, *C. viscaciae* is also found in a South American rodent. Consequently, *Cittotaenia rhea* is here assigned provisionally to the genus *Moniezia* pending a detailed review of the group, when, hopefully, the true associations of the parasite can be established.

The specific name given by Fuhrmann in 1904 was *rhea* however, in 1908 and 1932 Fuhrmann gave it as *rheae*, leading to some confusion in the subsequent literature. The original name, *rhea*, is used in the current review.

Following the initial collection, the parasite has been reported only from rheas in an American zoo (Keahey and Trapp, 1969).

Source : MNHN, Paris

TABLE 16. — MEASUREMENTS OF *MONIEZIA RHEA* (in mm)

	Fuhrmann (1904)	Fuhrmann (1921)	Present description	
			Types	*New material*
Length	50-90	50-90	—	115-228
Width	3	3	—	3-6
Scolex diam.		1.2	1.03-.146	1.2-1.3
Sucker diam.		0.7 × 0.55	0.62-0.78 × 0.52-0.58	0.70-0.75 × 0.50
Neck		1.7-2.3		0
Mature proglottis			1.9 × 0.4	2.3 × 0.13
Gravid proglottis			3.0 × 0.4	3.0 × 0.32
Cirrus sac	0.6 × 0.02	0.4 × 0.06	0.29-0.9 × 0.026-0.1	0.38 × 0.02
No. testes	approx. 110	approx. 100	approx. 100	approx. 120
Testis size		0.05-0.06	0.05	0.02-0.06 × 0.1
Seminal receptacle				0.06-0.3 × 0.03-0.13
Ovary		0.5	0.26-0.36 × 0.16-0.21	0.32-0.40 × 0.05-0.10
Vitellarium		0.19	0.12 × 0.08	0.01-0.15 × 0.03-0.04
Dorsal osmoregulatory canal			0.013 (neck)	—
Ventral osmoregulatory canal		0.06-0.08	0.026-0.039	0.05-0.14
Egg		0.070	0.055	0.06
Pyriform apparatus		0.010-0.012	0.035	—
Oncosphere			0.012-0.013	0.01

Moniezia bequaerti (Vigueras, 1943) comb. nov.
Figs 91-97, Table 17.

Cittotaenia bequaerti Vigueras, 1943 : 11-13 (as *bequarti* or *bequaerti*), figs 12-15.
Cittotaenia becquarti Lopez-Neyra, 1954 : 113.
Pseudocittotaenia bequaerti (Vigueras, 1943) Tenora, 1976 : 15.

TYPES. From *Capromys pilorides* (Say, 1882) (Rodentia : Capromyidae), Havana, Santa Clara and Matanzas, Cuba. Paratype in USNM.

MATERIAL EXAMINED. 6 specimens from *Capromys pilorides*, Cuba, 1959, J. G. Baer, UN; paratype.

DESCRIPTION. Small, narrow cestodes. Scolex large, conical in dorso-ventral view, with base of cone directed anteriorly. Suckers large, muscular, cup-shaped, anteriorly directed, situated at anterior extremity of scolex. Scolex merges imperceptibly into elongate neck. Proglottides craspedote, with narrow, straight-edged velum overhanging adjacent proglottis, extended transversely.

Source : MNHN, Paris

Mature proglottides with approximate length : width ratio of 1 : 4. Gravid proglottides with ratio of 1 : 2. Longitudinal musculature weakly developed, consisting of two rings of large diameter fibres around inner region of cortex. Fibres occasionally grouped in twos or threes but never in larger bundles. Transverse muscles fine, in band internal to longitudinal muscles. Dorso-ventral muscles fine, few in number, irregularly arranged. Longitudinal osmoregulatory canals paired. Ventral canal wider than dorsal canal, lying internal to dorsal canal. Transverse canal connects left and right ventral canals at posterior margin of each proglottis. Genitalia paired. Genital ducts pass longitudinal osmoregulatory canals dorsally. Genital atrium shallow, situated in middle of lateral proglottis margin. Cirrus sac short, oblong, thick-walled, reaching longitudinal osmoregulatory canals. Cirrus uncoiled, unarmed. Internal and external seminal vesicles absent. Vas deferens thin-walled, highly convoluted. Vasa efferentia not seen. Testes numerous, extending through most of proglottis medulla. Distribution of testes limited laterally by longitudinal osmoregulatory canals. Testes absent anterior to ovaries and genital ducts, arranged in 1-2 transverse and 5-8 longitudinal rows on dorsal aspect of medulla. Vagina narrow, thin-walled, opening to genital atrium posterior to cirrus sac. Vagina lies ventral to cirrus sac on right hand side of strobila, dorsal to it on left hand side. Seminal receptacle elongate, clavate, dorsal to ovary. Ovary fan-shaped, composed of numerous clavate lobules, situated on ventral aspect of medulla in anterior half of proglottis close to longitudinal osmoregulatory canals. Vitellarium oval or sub-triangular, posterior and dorsal to ovary. Mehlis' gland spherical, situated between ovary and vitellarium. Uterus net-like at commencement of development, extending over entire area of medulla. Islands of parenchyma between uterine strands disappear as uterus fills. Gravid uterus sac-like, filling proglottis. Egg spherical, thick-shelled. Oncosphere surrounded by pyriform apparatus, terminating in two elongate horns.

REMARKS. A single type specimen was available for study, as well as the material described above from the type host and locality. The description differs from that given by Vigueras (1943) in that the cirrus armature he described was not found. The original description states that the testes do not lie external to the longitudinal osmoregulatory canals (" pero no traspasan los vasos excretores ") however fig. 13 accompanying his description clearly shows some 15 testes lateral to the osmoregulatory canals on each side of the strobila. The drawing is apparently in error as no testes were found lateral to the osmoregulatory canals in the material redescribed above.

In spite of the fact that Vigueras (1943) described the developing uterus as reticulate (" uterus con ramificaciones simples haciendos sacciformes con lobulaciones ") he still placed the new species in the genus *Cittotaenia*. The structure of the uterus in this species is typical of the genera *Moniezia* and *Diandrya* Darrah, 1930, and is assigned to the former as it lacks seminal vesicles and a prostate gland, the presence of which characterises the genus *Diandrya*. Using Spasskii's key (1951), *M. bequaerti* belongs to the sub-genus *Baeriezia* Skrjabin and Schulz, 1937 since it lacks interproglottidal glands. It is easily distinguished from *M. baeri* Skrjabin, 1931 by its small size and from *M. mettami* Baylis, 1934 by the lack of a vaginal sphincter. *M. bequaerti* most closely resembles *M. rugosa* (Diesing, 1850) a parasite from South American primates, however the two species can be distinguished from one another by the number of testes per proglottis and by the presence of a vaginal sphincter in *M. rugosa*.

M. bequaerti is the first species of this genus to be recorded from rodents. With the exception of *M. rugosa* and *M. rhea* comb. nov. all other species of the genus are parasites of herbivora.

In Vigueras' original description (1943), the specific epithet is spelt *bequaerti* in the discussion and in the captions to the figures, in honour of a Dr. Bequaert, however, at the heading of the description it is given as *Cittotaenia bequarti* sp. nov. Since this is a typographical error rather than an intentional omission of the e, the name *bequaerti* has been used above.

Source : MNHN, Paris

TABLE 17. — MEASUREMENTS OF *MONIEZIA BEQUAERTI* (in mm)

	Vigueras (1943)	Present description
Length	120-210	up to 210
Width	4.7	5
Scolex diameter	1.5 × 1.8	1.10-.135
Sucker diameter	0.42	0.45-0.60
Neck		1.0-1.5
Mature proglottis	4.0-4.8 × 1.0-1.3	2.8-3.2 × 0.7-0.8
Gravid proglottis	2.0 × 2.5-3.0	2.6-4.4 × 1.5-2.2
Cirrus sac	0.24-0.28 × 0.065-0.080	0.2-0.3 × 0.06-0.07
No. testes	200-240	approx. 150
Testis size	0.48-0.56	0.07
Seminal receptable		0.20-0.45 × 0.09-0.25
Ovary		0.20-0.25 × 0.09-0.16
Vitellarium		0.11-0.16 × 0.10-0.15
Mehlis' gland		—
Dorsal osmoregulatory canal		0.04
Ventral oremoregulatory canal		0.07
Egg	0.054-0.058	0.07
Pyriform apparatus		0.045
Oncosphere	0.012-0.016	0.020

SPECIES INCERTAE SEDIS

Cittotaenia tachyglossi
Figs 98-102, Table 18.

Cittotaenia tachyglossis Johnston, 1913 : 75, 77-78, figs 1-3.

TYPES. From *Tachyglossus aculeatus* Shaw, 1792, Townsville, Queensland, Australia, 1911, whole mounts, spirit material and serial section, UAHC 1115, 1122.

MATERIAL EXAMINED.

From *Tachyglossus aculeatus* Shaw, 1792. Types ; fragments of several specimens, Townsville, Queensland, 1912, P. A. Maplestone, LSTM.

Source : MNHN, Paris

DESCRIPTION. Small cestodes. Scolex unarmed, approximately hemispherical, merging into neck region. Suckers hemispherical, thick-walled, embedded in scolex, openings directed anteriorly and laterally. Proglottides craspedote with narrow, mainly straight-edged velum overhanging adjacent proglottis, extended transversely. Mature proglottides with approximate length : width ratio of 1 : 4. Longitudinal musculature moderately developed, arranged in two rings of muscle bundles around cortex. Bundles small with few fibres. Fibres of inner bundle ring larger than those of outer ring. Transverse muscles fine, in band internal to longitudinal muscles. Dorso-ventral muscles very fine, sparse, crossing cortex and medulla at irregular intervals. Longitudinal osmoregulatory canals paired. Ventral canal slightly wider than dorsal canal, lying internal to dorsal canal. Transverse canal connects left and right ventral canals at posterior margin of each proglottis. Anterior to suckers, transverse anastomosis connects ventral canals from either side. Similar anastomosis joins dorsal canals. Four canals continue anteriorly from anastomoses. On each side of strobila, short dorso-ventral loop connects dorsal and ventral canals. Genitalia paired. Genital ducts cross longitudinal osmoregulatory canals ventrally. Genital atrium small, situated in middle of lateral proglottis margin. Cirrus sac narrow elongate, extending beyond osmoregulatory canals. Cirrus slightly coiled, unarmed. Proximal extremity of cirrus sometimes slightly dilated. Internal and external seminal vesicles absent. Vas deferens thin-walled, greatly coiled near proximal pole of cirrus sac, passing posteriorly, dorsal to ovary. Vasa efferentia not seen. Testes numerous, scattered throughout proglottis medulla on dorsal aspect, overlying female genitalia and occasionally lying just lateral to longitudinal osmoregulatory canals. Testes in single dorso-ventral layer. Vagina opens to genital atrium posterior to cirrus sac. Prominent, discrete, muscular sphincter present at distal extremity of vagina. Seminal receptacle absent. Ovaries situated in lateral quarters of proglottis medulla, on ventral aspect, fan-shaped, composed of numerous clavate lobules. Vitellarium posterior and dorsal to ovary, narrow elongate, extending medially almost to midline of proglottis. Mehlis' gland anterior to vitellarium at apex of ovary. Uterine duct emerges from Mehlis' gland on dorsal aspect, runs anteriorly to beyond anterior margin of ovary, terminating in slight enlargement. Uterus not seen. Gravid proglottides not present.

REMARKS. Although incomplete, the present description extends that of Johnston (1913) as well as recording Maplestone's collection from the type host and locality of apparently the same species. Johnston's description is in error in stating that the genital ducts pass the osmoregulatory canals dorsally, but the error is probably due to the fact that Johnston did not prepare sections of the parasite.

Apart from the fact that *C. tachyglossi* has paired genitalia, it is very similar to the single-pored species *Linstowia echidnae* (Thompson, 1893) from the same host species. The position of the genital ducts ventral to the osmoregulatory canals and the aporally extended vitellarium are both characteristics of *L. echidnae*, the latter feature occurring only in this species. The similarities pointed out suggest that *C. tachyglossi* probably represents a new genus in the family Linstowiidae, however, the form of the uterus is not known and it is considered best to leave the parasite under its present name pending collection of gravid specimens and the completion of the description.

If the above suggested taxonomic position is correct, it is probable that *C. tachyglossi* developed from *L. echidnae* by duplication of the genitalia, as has been suggested for other cestodes (Baer, 1927, Spasskii, 1951, Baer, 1955).

Source : MNHN, Paris

TABLE 18. — MEASUREMENTS OF *CITTOTAENIA TACHYGLOSSI* (in mm)

	Johnston, 1913	Present study (From types)
Length (fragments)	11	24
Width	0.56	2.0
Scolex diameter	0.56	0.65-0.79
Sucker diameter	0.13	0.21-0.28
Neck		0.6-1.1
Mature proglottis		2.2 × 0.4
Cirrus sac	0.2 × 0.033-0.05	0.43-0.50 × 0.04-0.06
No. testes per proglottis		approx. 200
Testis size	0.015	0.03-0.05
Ovary		0.24 × 0.16
Vitellarium		0.45 × 0.04
Mehlis' gland		0.06
Dorsal osmoregulatory canal		0.01
Ventral osmoregulatory canal		0.02

SPECIES INQUIRENDAE

Cittotaenia quadrata

Cittotaenia quadrata von Linstow, 1904, : 680-681, figs 3-4.
Ctenotaenia quadrata (von Linstow, 1904) Spasskii, 1951 : 271, fig. 127.
Neoctenotaenia quadrata (von Linstow, 1904) Tenora, 1976 : 13.
Cittotaenia pectinata (Goeze, 1782) pro parte Baer, 1927 : 55.

TYPES. From *Lagidium peruanum* Meyen, 1833, Peru. Slides of serial sections in UN.

MATERIAL EXAMINED. Types.

REMARKS. The type material is in too poor a state to permit redescription and the original description is inadequate to determine satisfactorily the taxonomic position of the parasite. As indicated earlier, *C. quadrata* may be similar to *C. viscaciae* and they may even come from the same host, however, the matter cannot be taken further without fresh material.

Cittotaenia dratchynskii

Cittotaenia dratchynskii Romanovich, 1915 : 451.
Moniezia ? dratchyuskii (Romanovich, 1915) López-Neyra, 1954 : 121.

TYPES. From *Rangifer tarandus* Linnaeus, 1758, Western Siberia, present whereabouts unknown.

Source : MNHN, Paris

Cittotaenia krishnai Nama, 1972

Cittotaenia krishnai Nama, 1972 : 52-53, fig. 1.

TYPES. From *Capra hircus* Linnaeus, 1758, Jodhpur, India.

REMARKS. Unfortunately, the types of this species have been lost (H. S. Nama, personal communication), and as it is impossible to determine the position of this species from the original description, it must be placed as a *species inquirenda*.

DISCUSSION

The present review, together with an earlier revision of the anoplocephalid cestodes of Australian marsupials (Beveridge, 1976) constitute a revision of most of the genera of anoplocephaline cestodes with paired genitalia parasiting mammals. Only two genera have been neglected, *Ectopocephalium* Rausch and Ohbayashi, 1974 and *Diuterinotaenia* Gvozdev, 1961, both of which are monotypic, recently and adequately described and with characteristic morphological features which would prevent their confusion with other genera. A third genus *Eranuides* Semenova, 1972 based on two incomplete specimens from a reindeer was initially placed in the subfamily Anoplocephalinae (Semenova, 1972) though the morphology of the mature proglottis is remarkably similar to that of species of *Moniezia*. Tenora (1976) transferred the genus to the sub-family Monieziinae.

The various genera described in this review, their component species and related genera together with their distinguishing characteristics are set out in Table 19 and a key to them is provided below.

As suggested by Beveridge (1976), provided patterns of infra-specific variation are taken into account, the distribution of the testes within the proglottis provides important generic criteria within the sub-family under consideration. The structure of the vagina and seminal receptacle was also found to be characteristic for a genus in several instances and may be of greater taxonomic value than realised in the past.

The present revision has shown that the parasites of the "*Cittotaenia*" complex" are exclusively parasites of mammals. Species previously placed in this group from avian hosts have invariably had to be removed to other genera or subfamilies following redescription. As indicated in Table 19, each genus is, for the most part restricted to one family of host species, although minor exceptions do exist. Although not taken into account in the taxonomy of the parasites the finding that related parasites share similar hosts suggests that the classification presented conforms to some extent to what one might expect of a "natural classification".

In view of the relatively extensive literature on the phylogeny of the Anoplocephalinae (see Baer, 1927, Spasskii, 1951, Tenora, 1976) the present revision requires that some comment be made on the validity of earlier theories. The possible phylogeny of the Australian genera has been discussed by Beveridge (1976).

Spasskii (1951) argued that the genera *Mosgovoyia* and *Ctenotaenia* arose by duplication of the genitalia of members of the genera *Schizorchis* Hansen, 1948 and *Paranoplocephala* Lühe, 1910 respectively. The argument was based on the fact that in the genera *Schizorchis* and *Mosgovoyia*, both parasites of lagomorphs (Ochotonidae and Leporidae respectively), the testes lie entirely posterior to the uterus. In spite of the substantial changes to the genus *Mosgovoyia* made in the present revision, the retention of the occurrence of testes posterior to the uterus as a key generic character in no way contradicts Spasskii's hypothesis. The present inclusion of all of the anoplocephaline cestodes of leporids in one genus rather strengthens the hypothesis.

Similarly, the changes in the composition of the genus *Ctenotaenia* in no way invalidate the basic hypothesis. Although species of the rodent genera *Marmota* and *Citellus* are found in North

Source : MNHN, Paris

America as well as Europe and Asia, *Ctenotaenia marmotae* appears to be a strictly Eurasian species as investigations of the parasites of marmots in North America have not revealed its presence there (Darrah, 1930, Philip, 1938, Rausch, 1951). Species of *Paranoplocephala* occur in Eurasian marmots (*P. transversaria* (Krabbe, 1879) and *P. ryjikovi* Spasskii, 1950) which have a uterus limited to the cortex during the entire course of its development and in which the testes are disposed aporally to the female genitalia but both anterior and posterior to the uterus, characteristics which are also present in *Ct. marmotae*. In fact, duplication of a proglottis of the type found in these species of *Paranoplocephala* gives precisely the morphological features of *Ct. marmotae*.

In certain North American species of *Paranoplocephala*, such as *P. troeschi* Rausch, 1946 the testes are again limited to the region aporal to the female genitalia, but they are entirely posterior to the uterus which is at the anterior extremity of the proglottis and which crosses the longitudinal osmoregulatory canals ventrally, terminating anterior to the cirrus sac. Duplication of such a proglottis would give almost exactly that of a species of *Pseudocittotaenia* and since the features of the uterus in this latter genus are totally different to those found in related genera with paired genitalia, it seems reasonable to suggest that the genus *Pseudocittotaenia* arose in this fashion, by a duplication of genitalia, in a manner parallel to *Ct. marmotae* in Europe and Asia.

Spasskii (1951) and Tenora (1976) considered the subfamily Monieziinae to be " phylogenetically younger " than the sub-family Anoplocephalinae and in particular, the genus *Cittotaenia* was considered to have arisen by duplication of the genitalia of species of *Andrya* Railliet, 1893 (see Tenora, 1976). This hypothesis seems unlikely as the uterus of *C. denticulata* is scarcely reticulated whilst that of species of *Andrya* is net-like. Furthermore, the genus *Diandrya* Darrah, 1930 seems to be a far more logical product of the duplication of the genitalia of species of *Andrya*. The present revision gives little or no clue as to the phylogenetic affinities of the genus *Cittotaenia*. In the writer's opinion, it would be better to refrain from speculating upon the matter until the systematics are better understood and until a reasonable hypothesis presents itself.

TABLE 19. — RELATIONSHIPS OF THE GENERA OF ANOPLOCEPHALINE CESTODES WITH PAIRED GENITALIA PARASITISING MAMMALS AND THE MONIEZIINE GENUS *CITTOTAENIA*.

Genus and Species	*Hosts*	*Characteristic feature(s)*	*Reference*
Cittotaenia Riehm, 1881			
C. denticulata *C. viscaciae*	Lagomorphs (Leporidae) and rodents (Cbinchillidae)	Uterus slightly reticulate, with anterior and posterior diverticula	
Ctenotaenia Railliet, 1893			
Ct. marmotae	Rodents (Sciuridae)	Testes anterior and posterior to uterus, between female genitalia	
Diuterinotaenia Gvozdev, 1961			
D. spasskii	Lagomorphs (Ochotonidae)	Uteri paired, arranged longitudinally	Gvozdev (1961)
Ectopocephalium Rausch and Ohbayashi, 1974			
E. abei	Lagomorphs (Ochotonidae)	Long neck, scolex covered in glands	Rausch and Ohbayashi (1974)

Source : MNHN, Paris

Genus and Species	*Host*	*Characteristic feature(s)*	*Reference*
Mosgovoyia Spasskii, 1951			
M. pectinata *M. ctenoides* *M. variabilis*	Lagomorphs (Leporidae)	Testes entirely posterior to uterus, uterus restricted to medulla or terminating in cortex posterior to cirrus sac	
Paramoniezia Maplestone and Southwell, 1923			
P. suis *P. johnstoni*	? Pigs (Suidae) and marsupials (Vombatidae)	Testes scattered throughout medulla, seminal receptacle large, pyriform, merging into vagina.	Beveridge (1976)
Phascolotaenia Beveridge, 1976			
P. comani	Marsupials (Vombatidae)	Most testes posterior to uterus, two small groups anterior to uterus near osmoregulatory canals. Seminal receptacle as in *Progamotaenia*	Beveridge (1976)
Progamotaenia Nybelin, 1917			
P. bancrofti *P. aepyprymni* *P. diaphona* *P. effigia* *P. eversi* *P. festiva* *P. lagorchestis* *P. proterogyna* *P. villosa* *P. zschokkei*	Marsupials (Macropodidae and Vombatidae)	Testes anterior to uterus, extending lateral to female genitalia. Vagina narrow, seminal receptacle circular	Beveridge (1976)
Pseudocittotaenia Tenora, 1976			
P. praecoquis *P. glandularis*	Rodents (Geomyidae)	Uterus anterior to testes, crosses osmoregulatory canals ventrally, terminates anterior to cirrus sac.	

KEY TO GENERA OF ANOPLOCEPHALINE CESTODES WITH PAIRED GENITALIA PARASITISING MAMMALS

1. Uterus paired, longitudinal..... *Diuterinotaenia*
   Uterus single or paired, transverse..... 2
2 (1). Neck extremely long, scolex embedded in diverticulum of host's intestine, scolex covered with glands. *Ectopocephalium*
   Neck short or absent, parasite restricted to lumen of intestine or biliary system, scolex without glands. 3
3 (2). Uterus in tubular stage extends beyond osmoregulatory canals ventrally, terminating anterior to level of cirrus sac. Uterus at anterior extremity of proglottis..... *Pseudocittotaenia*

Source : MNHN, Paris

Uterus not at anterior extremity of proglottis. Either restricted to medulla in tubular stage, or if not, then crosses osmoregulatory canals dorsally, terminating in cortex posterior to cirrus sac and vagina..... 4

4 (3). Testes restricted to region between female genitalia, lying both anterior and posterior to uterus.... *Ctenotaenia*

Some testes lying poral to female genitalia, or if restricted to area between genitalia, then entirely posterior to uterus 5

5 (4). Testes in single band or two groups entirely posterior to uterus..... *Mosgovoyia*

Testes entirely or in part anterior to uterus..... 6

6 (5). Testes arise in single band or two groups anterior to uterus..... *Progamotaenia*

Some testes posterior to uterus..... 7

7 (6). Testes distributed througbout medulla..... *Paramoniezia*

Testes in band posterior to uterus with two small groups anterior to uterus, in lateral extremities of proglottis medulla..... *Phascolotaenia*

Source : MNHN, Paris

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Source : MNHN, Paris

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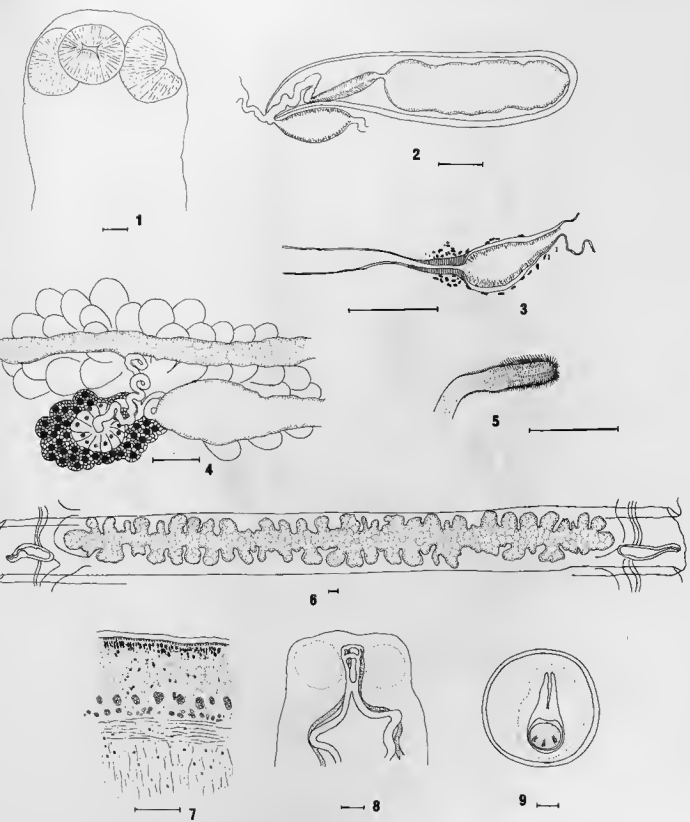
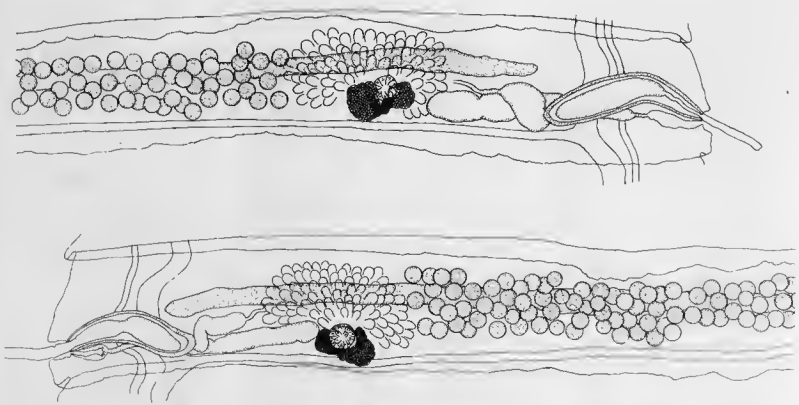


Ctenotaenia marmotae. Figs 1-10.

1. Scolex; 2. Cirrus sac; 3. Histological section of distal extremity of vagina showing vaginal atrium; 4. Female genital complex; 5. Everted cirrus showing armature; 6. Gravid proglottis; 7. Transverse histological section of strobila showing musculature; 8. Scolex showing osmoregulatory system; 9. Egg.

Source : MNHN, Paris

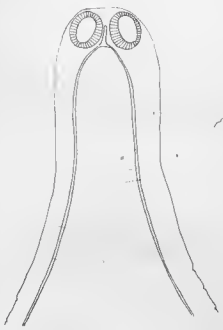


10

10. Mature proglottis.

Scale lines : 0.1, except fig. 9, 0.01 mm.

Source : MNHN, Paris



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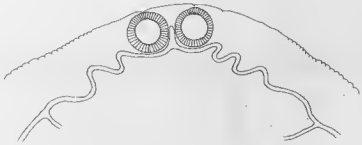

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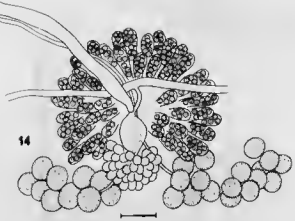

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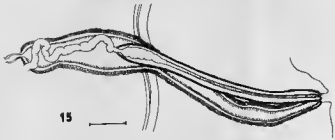

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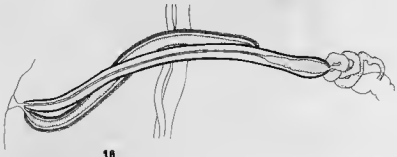
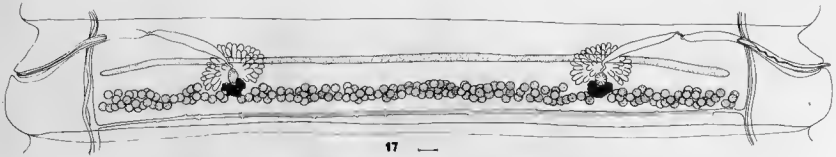


16

Musgravoyia pectitata. Figs 11-25.

11. Scolex of relaxed specimen; 12. Scolex from type specimen of *Cittotaenia bursaria* von Linstow, 1906 (now a synonym of *M. pectinata*) showing effects of severe contraction on scolex; 13. Transverse histological section through strobila showing musculature; 14. Female genital complex; 15. Cirrus sac and distal vagina from specimen from *Oryctolagus cuniculus*, England; 16. Cirrus sac and vagina from specimen from *Lepus americanus* from North America showing extent of variation in length of cirrus sac with respect to vagina.

Source : MNHN, Paris



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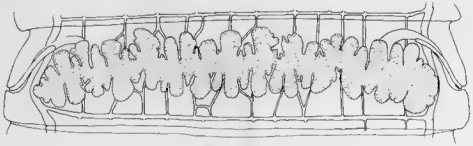
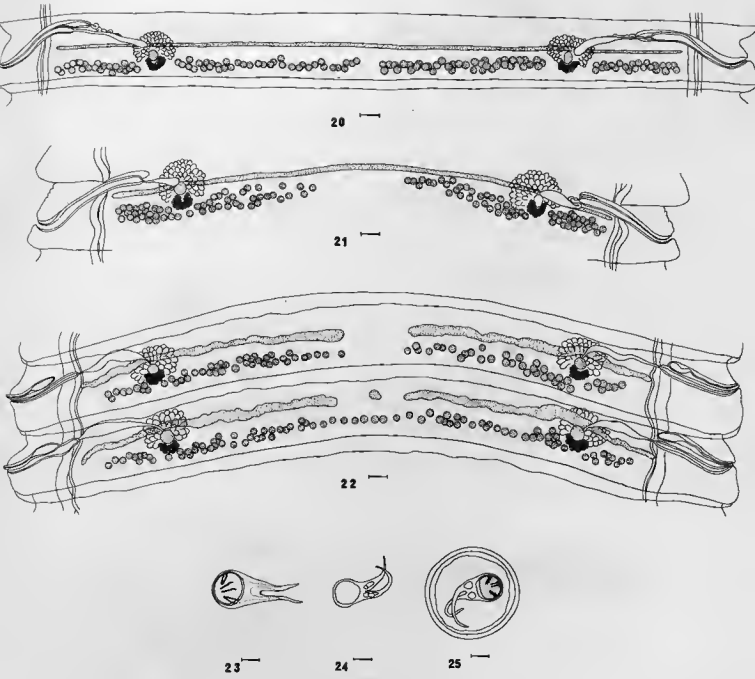


19 —

17-19. Specimens from *Oryctolagus cuniculus*, England. 17. Mature proglottis; 18. Pre-gravid proglottis with paired uteri; 19. Gravid proglottis showing accessory osmoregulatory canals.

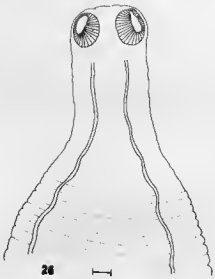
Source : MNHN, Paris

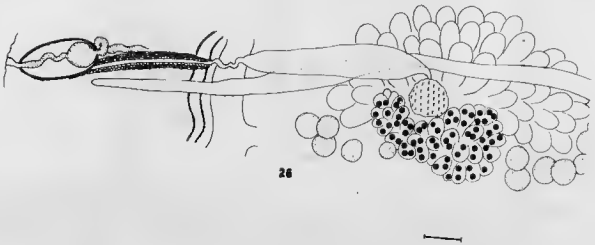


20. From *Lepus townsendi*, USA, USNM 59076, mature proglottis showing slight break in band of testes; 21. From *Lepus californicus*, USA, USNM 59259, mature proglottis showing complete separation of the testes into 2 lateral groups; 22. From *Sylvilagus nuttalli grangeri*, USA, USNM 59073, two adjacent proglottides from strobila showing variation in testis distribution between proglottides of one worm; 23. Normal embryo and pyriform apparatus; 24. Pyriform apparatus showing (as in fig. 25) vacuolations within arms; 25. Egg.

Scale lines : figs 11-23, 0.1 mm; figs 23-25, 0.01 mm.

Source : MNHN, Paris

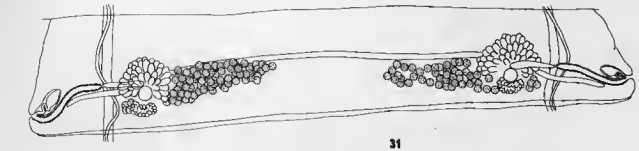




Mongovoyia etewaides. Figs 26-34.

26. Scolex of relaxed specimen; 27. Scolex of partly contracted specimen showing constriction behind suckers and reduction in length of neck; 28. Transverse section of strobila showing musculature; 29. Genital ducts and female genital complex; 30. Egg.

Source : MNHN, Paris



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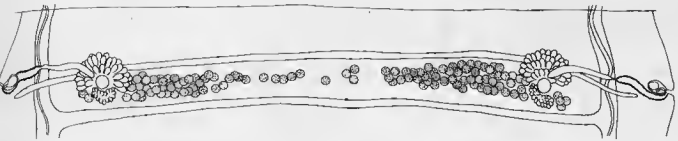

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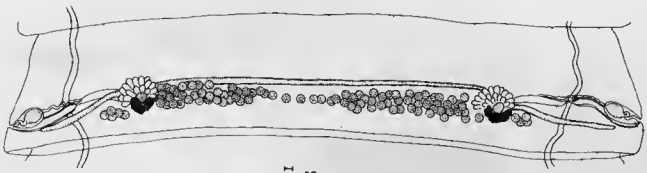

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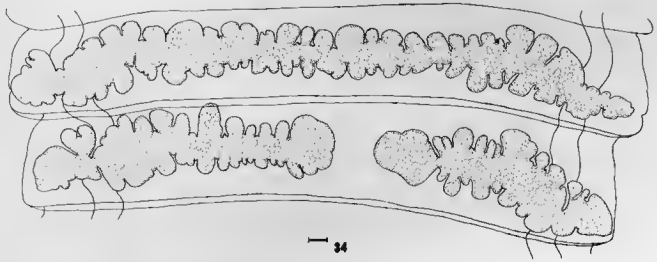
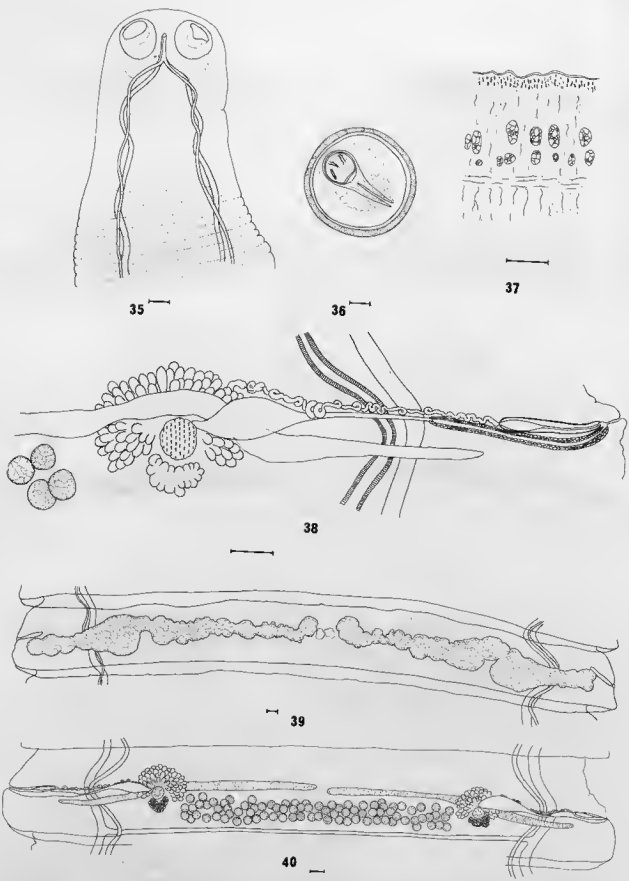


34

31-33. Mature proglottides showing variation in testis distribution; 34. Gravid proglottides showing proglottides with single or paired uterus.

Scale lines : figs 26-29, 31-34, 0.1 mm; fig. 30, 0.01 mm.

Source : MNHN, Paris



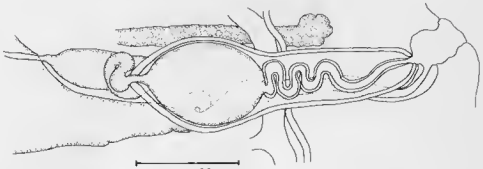
Mosgovoyia variabilis. Figs 35-40.

35. Scolex; 36. Egg; 37. Transverse histological section of strobila showing musculature; 38. Genital ducts and female genital complex; 39. Gravid proglottis; 40. Mature proglottis.

Scale lines : figs 35, 37, 38-40, 0.1 mm; fig. 36, 0.01 mm.

Source : MNHN, Paris

41



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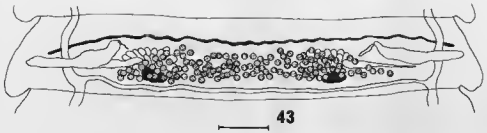

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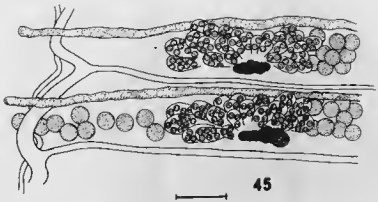
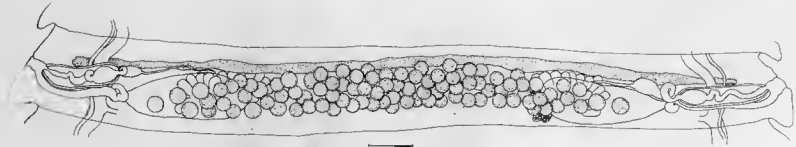


45

Pseudocittotaenia praecoquis. Figs 41-47.

41. Scolex; 42. Cirrus sac and distal vagina, dorsal view, showing uterus crossing the osmoregulatory canals ventrally and terminating anterior to cirrus sac; 43. Pre-mature proglottis showing distribution of testes posterior to uterus; 44. Egg; 45. Lateral part of two proglottides, ventral view, showing variation in testis distribution within worm.

Source : MNHN, Paris



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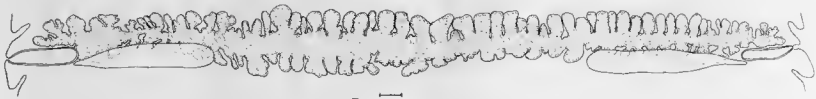

47

46. Mature proglottis; 47. Gravid proglottis.
Scale lines : figs 41-43, 45-47, 0.1 mm; fig. 44, 0.01 mm.

Source : MNHN, Paris

51

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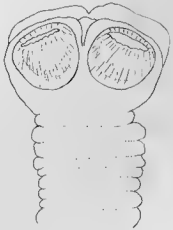


48

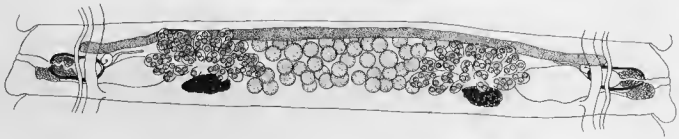
Pseudocittotaenia glandularis. Figs 48-51.

From holotype from *Thamnomys talpoides*. Fig. 48. From other material from same host species.

48. Scolex; 49. Cirrus sac and distal vagina; 50. Egg; 51. Gravid proglottis.

Source : MNHN, Paris

52

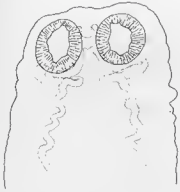


53

54

52. Pre-mature proglottis ; 53. Mature proglottis ; 54. Post-mature proglottis.
Scale lines : figs 48, 49, 51-54, 0.1 mm ; fig. 50, 0.01 mm.

Source : MNHN, Paris



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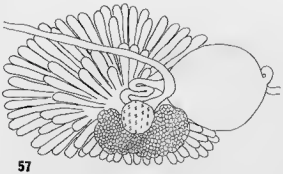

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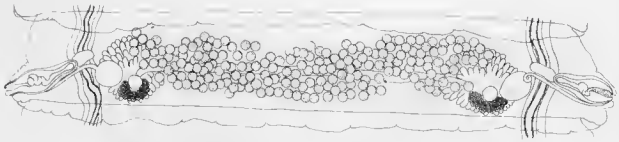
60

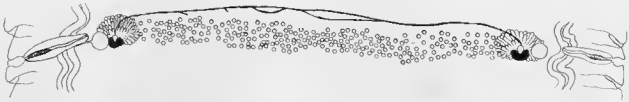
Cittotaenia denticulata. Figs 55-63.

55. Scolex showing osmoregulatory system; 56. Cirrus sac; 57. Female genital complex; 58. Egg; 59. Embryo with three armed pyriform apparatus; 60. Lateral region of proglottis showing osmoregulatory system; 61. Transverse histological section of strobila showing musculature.

Source : MNHN, Paris



62



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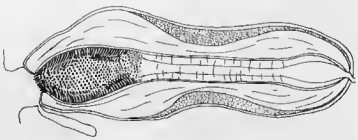
62. Mature proglottis; 63. Premature proglottis showing uterus; 64. Uterus during development showing slight reticulations and the formation of diverticula; 65. Gravid uterus.

Scale lines : figs 55-57, 60-65. 0.1 mm; figs 58. 59, 0.01 mm.

Source : MNHN, Paris

66



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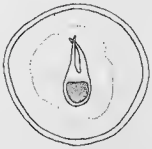


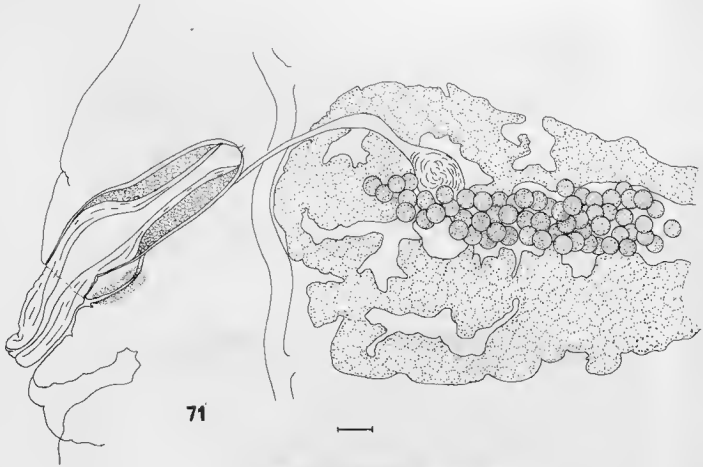
69

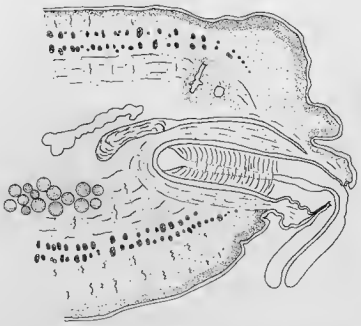
70

Cittotaenia viscaciae. Figs 66-72. All drawings from type.

66. Scolex; 67. Cirrus sac; 68. Mature proglottis; 69. Egg; 70. Genital ducts and female genital complex.

Source : MNHN, Paris

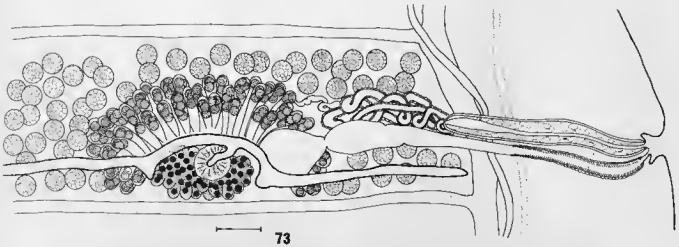




71. Longitudinal section of proglottis showing reticulated uterus; 72. Transverse section of proglottis showing musculature and disposition of various genital organs.

Scale lines : Figs 66-68, 70-72, 0.1 mm; fig. 69, 0.01 mm.

Source : MNHN, Paris



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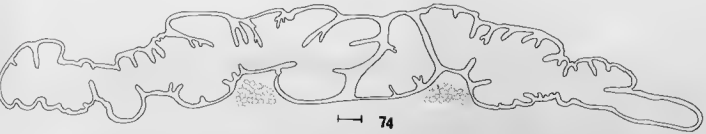


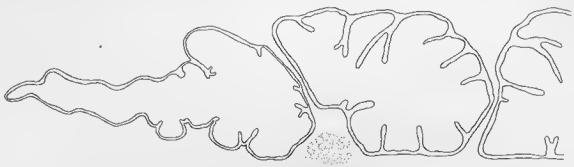
74

75

Stringopotaenia psittacea. Figs 73-78. All drawings from type.

73. Lateral region of mature proglottis reconstructed from serial sections; 74. Histological section of gravid uterus; 75. Egg.

Source : MNHN, Paris



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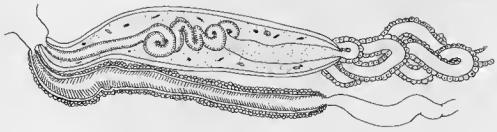

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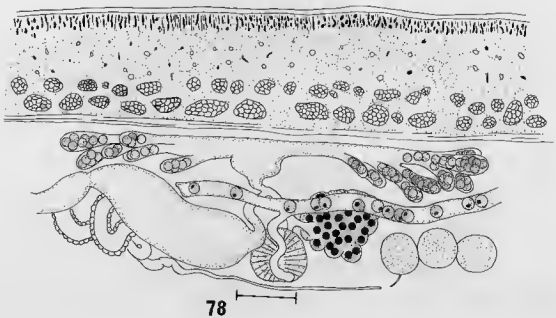
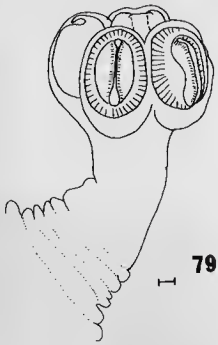


78

76. Histological section of portion of gravid uterus; 77. Cirrus sac and distal vagina; 78. Transverse histological section showing musculature and genital organs.

Scale lines : figs 73, 74, 76-78, 0.1 mm; fig. 75, 0.01 mm.

Source : MNHN, Paris



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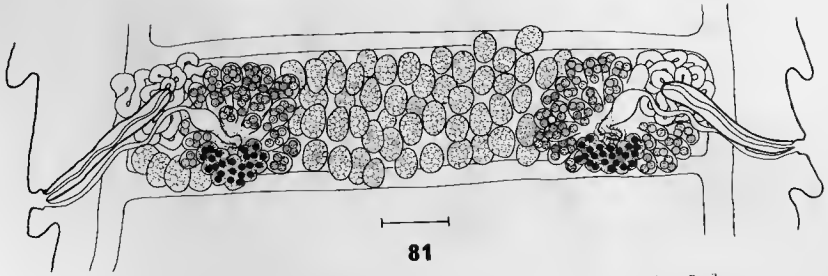
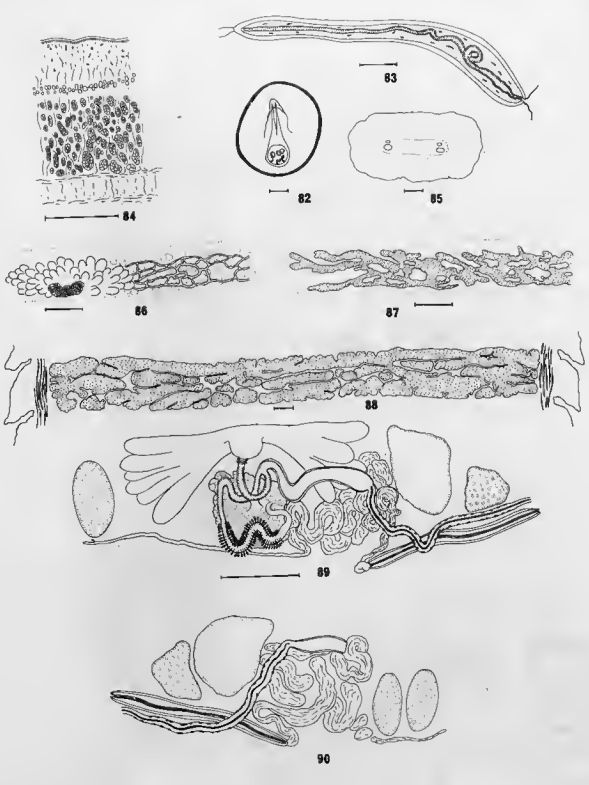


81

Moniezia rhea. Figs 79-90. Figs 79-83 from types, remainder from specimens from *Rhea americana*, Brazil.

79. Scolex; 80. Egg showing partial development of pyriform apparatus; 81. Mature proglottis, reconstructed from serial sections.

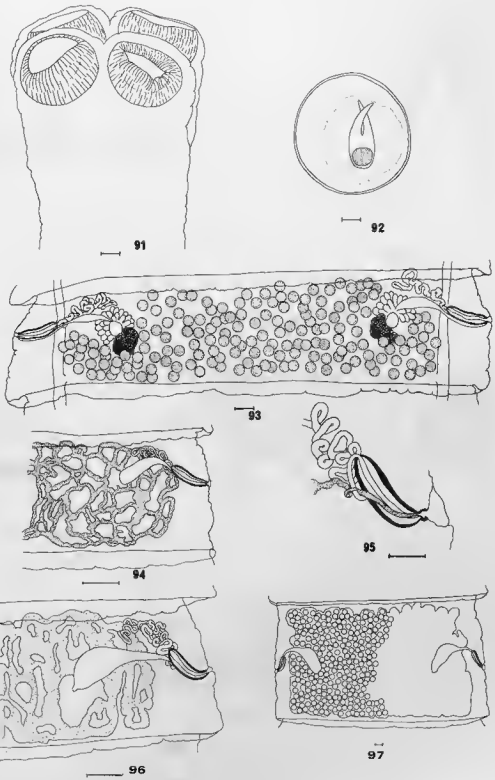
Source : MNHN, Paris



82. Egg with fully developed pyriform apparatus; 83. Cirrus sac; 84. Transverse histological section showing musculature; 85. Transverse histological section of neck showing presence of two pairs of longitudinal osmoregulatory canals; 86. Longitudinal histological section of mature proglottis showing reticulated uterus; 87. Longitudinal histological section of mature proglottis showing reticulated uterus; 87. Longitudinal histological section of post mature proglottis showing developing uterus; 88. Longitudinal histological section through uterus of gravid proglottis; 89. Transverse histological section of mature proglottis showing genitalia, right hand side of proglottis; 90. Transverse histological section of left hand side of proglottis showing genital ducts.

Scale lines : figs 79-80, 83-90, 0.1 mm; figs 81, 82, 0.01 mm.

Source : MNHN, Paris

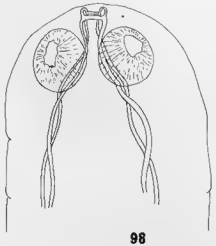


Moniezia bequaerti. Figs 91-97.

91. Scolex; 92. Egg; 93. Mature proglottis; 94. Lateral region of post-mature proglottis with developing, reticulated uterus; 95. Cirrus sac and distal vagina; 96. Subsequent stage of uterine filling with reduction in the number of reticulations; 97. Gravid uterus.

Scale lines : figs 91, 93-97, 0.1 mm; fig. 92, 0.01 mm.

Source : MNHN, Paris



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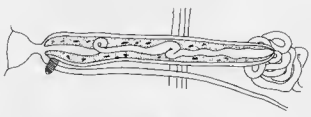

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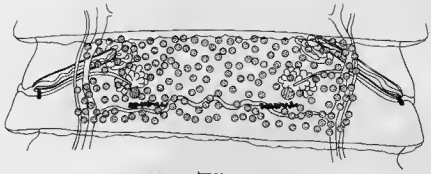

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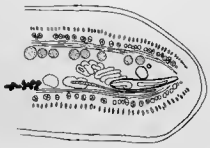

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Cittotaenia tachyglossi. Figs 98-102. All drawings from types.

98. Scolex; 99. Cirrus sac and distal vagina; 100. Mature proglottis; 101. Female genital complex; 102. Transverse histological section showing musculature and genital ducts.

Scale lines : 0.1 mm.

Source : MNHN, Paris

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